COMPETITION BETWEEN BROWN AND RAINBOW TROUT IN SCOTTS CREEK, A SPAWNING TRIBUTARY OF LAKE ALEXANDRINA

A thesis

presented for the degree of

Doctor of Philosophy in Zoology

in the

University of Canterbury,

Christchurch, New Zealand

by

JOHN HAYES

1984

CONTENTS

LIST OF TABLES

LIST OF PLATES

Plate

LIST OF FIGURES

ABSTRACT

Interference competition for spawning space, and competition for space between underyearlings, was studied in sympatric populations of brown and rainbow trout using Scotts Creek, the major spawning tributary of Lake Alexandrina, between November 1979 and September 1983.

Redd superimposition severely limited the spawning success of both species and favoured late spawning rainbow trout. The overall spawning success, from egg deposition to fry emergence, was 2.1% for rainbow trout and 0.2% for the earlier emerging brown trout. Redd superimposition caused a 94% reduction in the spawning success of brown trout in an experimental spawning section of Scotts Creek. Spawning of female rainbow trout was investigated with simple models to aid in understanding the relationships between arrival pattern of females, capacity for spawning space and associated redd superimposition, and pattern of fry emergence. The potential for competition for spawning space to influence timing of runs through selection acting on time of spawning was also considered.

The potential for competition for space between underyearlings in Scotts Creek was determined from an investigation of social interactions and microhabitat partitioning in stream observation troughs. Species and size appeared more important than prior residence in governing dominance relationships. Rainbow trout were socially dominant as fry in riffles, and after the fry stage brown trout were socially dominant in all microhabitats tested. Social conflict between fry and fingerlings was minimized by size dependent aggression, aggression being highest between fish of similar size.

Study of comparative abundance, migration and population dynamics of 0^+ brown and rainbow trout in Scotts Creek provided information for assessing the importance of competition between

underyearlings in the stream and its role in regulating populations of the two species in Lake Alexandrina. The juvenile salmonid populations in Scotts Creek were dominated by late emerging 0^+ rainbow trout despite a much greater tendency shown by brown trout to remain in the stream following emergence. Rainbow trout juvenile output from Scotts Creek was heavily dependent on recently emerged fry whereas that of brown trout was dependent more on fish which had undergone a period of stream residence. Competition between juvenile brown and rainbow trout was discussed in relation to the migratory strategies employed by each species with respect to lotic versus lentic rearing.

Competition between brown and rainbow trout was discussed in the context of competition and niche theories. Hutchinson's multidimensional hypervolume concept of the niche was shown to be inadequate for species such as freshwater fish which have multistage lifecycles. A modification to Hutchinson's model is proposed which takes into account the entire lifetime of a species with population regulatory mechanisms, including competition, potentially acting at various stages of the lifecycle.

The possibility of competitive exclusion of brown trout from Lake Alexandrina by rainbow trout is considered, and factors enabling coexistence in the face of severe competition for spawning space are discussed.

CHAPTER I

GENERAL INTRODUCTION

Competition has received considerable attention from ecologists in the past twenty-five years, the renewed interest arising from studies of the "ecological niche" and "competitive exclusion" in the first half of this century (Diamond 1978). Grinnell (1904,1908) was the first naturalist to express an appreciation of the concepts of the niche and competitive exclusion. However, sustained interest in competition did not develop until Lotka (1925) and Volterra (1926) had developed mathematical equations to model competition and Gause (1934) had demonstrated competitive exclusion in simple laboratory populations of ciliates. These and subsequent studies by laboratory ecologists (e.g., Crombie 1946, Park 1948) and by field ecologists (e.g., Lack 1945,1947, Elton 1946) led to the formulation of the concepts of the niche (see Hutchinson 1957) and competitive exclusion which together provide the basis for modern niche and competition theory. In broad terms the niche consists of the resources a species uses, where it finds them and the strategy by which it harvests them (Diamond 1978). Competition occurs when a number of animals (of the same or different species) utilize common resources the supply of which is short; or, if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one another in the process (Birch 1957). Competition can be by exploitation or by interference. In exploitative competition, individuals by using resources, deprive others of the benefits to be gained by those resources. Interference competition is more direct and occurs when individuals harm one another by fighting, producing toxins, destroying eggs or larvae etc.. Interspecific competition usually results in a reduction in the equilibrium population size of one or more of the

competing species and in extreme cases competitive exclusion of a species may occur. The competitive exclusion principle (Hardin 1960) (or Gause's principle) states that species must "occupy different niches" to coexist, because otherwise one species will competitively exclude the other.

Much of the evidence for competition presented in the past has been inferential rather than direct and this has resulted in a questioning of the importance of competition in community ecology by some authors (e.g. Connor and Simberloff 1979, and see review by Schoener 1982). Until recently, field experiments demonstrating interspecific competition have been rare (e.g., see review by Connell 1975). However the past five years has seen a rapid growth in such experiments, many of which have presented direct evidence for interspecific competition (see reviews by Schoener 1983 and Connell 1983). Schoener (1983, pg. 273) concludes that; "... interspecific competition has now been established experimentally in a great variety of natural systems and among a great variety of organisms". However, examination of the reviews by both Connell and Schoener reveals that the evidence for competition in freshwater systems is sparse, and particularly for freshwater fish.

Competition between freshwater fish must be considered in the context of their multistage lifecycles since often a different set of resources is utilized, and the potential for interspecific competition is likely to be different, at each stage. Although competition may be potentially important at any stage, its realization can be dependent upon population regulatory forces acting on the populations at an earlier stage. For example, adverse predation and physical conditions can reduce the abundance of potential competitors to a level where competition will not occur (Connell 1975). An additional possibility which has received little consideration is that competition it self acting at some stage in a species life cycle may, like predation and physical conditions,

determine the realization of competition at some later stage.

Situations in which interspecific competition might be expected to be most severe and most apparent, and therefore able to be demonstrated, arise when closely related but geographically isolated species are brought into unnatural sympatry by man. Such species may have considerable niche similarity but might not necessarily have mechanisms to alleviate interspecific competition with each other as they might with competitors in their native ranges. Two such species are brown trout (Salmo trutta Linnaeus) and rainbow trout (Salmo gairdneri Richardson) in New Zealand, where they occur in many lakes and rivers in unnatural sympatry. Brown trout (originally of English stock) and rainbow trout (apparently "steelhead" i.e., anadromous rainbow trout) were introduced into New Zealand in the late 1800s, from Tasmania and California respectively (MacCrimmon and Marshall 1968, MacCrimmon 1971, Scott and Fraser 1978). Depending on the system, either species can dominate in New Zealand waters. A review of the distribution of these two species in New Zealand, by Allen and Cunningham (1957), indicated that factors determining dominance are varied and complex, possibly involving climate, geology and ecology. As they are ecologically very similar, sympatric populations of brown and rainbow trout may experience severe interspecific competition, which in some systems may determine the balance between the species.

Freshwater fish may compete for food, space or spawning sites. Although competition for spawning sites will probably occur much less frequently than competition for food (or food-related space), its effects are liable to be considerably more damaging to a population (Larkin 1956).

Competition for spawning sites acts directly, by interference, on the population abundance of competing species, reducing the potential abundance of either or both species. Thus direct evidence of this form of

competition may be obtained. The results of an extensive survey of the efficiency of natural propagation of trout in New Zealand waters by Hobbs (1948) indicated that a number of trout populations in New Zealand were limited by redd superimposition. Redd superimposition is a type of interference competition for spawning site and occurs when a female in digging a redd in which to deposit her own eggs in the gravel of a stream bed disturbs or dislodges eggs deposited previously by other fish. In New Zealand, rainbow trout generally spawn later than brown trout. Thus, in waters where these two species occur in sympatry, and where suitable spawning areas are limited and spawner densities are high, dominance by rainbow trout might be favoured by interspecific competition for spawning space, mediated through redd superimposition. This situation is most likely to occur, and be detected, in physically stable waters.

A mixed population of brown and rainbow trout dominated by the latter species occurs in Lake Alexandrina, a high country lake in the South Island of New Zealand, The spawning areas in this system are limited and are utilized by large numbers of trout. Therefore interspecific competition for spawning space, mediated through redd superimposition, was investigated in the major spawning tributary of Lake Alexandrina, Scotts Creek, as a possible factor causing the dominance of rainbow trout in this system. Scotts Creek fulfilled all the prerequisites considered necessary for interspecific competition for spawning space to occur and be detected i.e., it had a limited physically stable spawning ground which was utilized by both brown and rainbow trout, with rainbows spawning later and in high densities. In addition, its small size and ease of access made such an investigation feasible.

I also investigated the potential for interspecific competition for space between underyearlings in the stream to determine its influence on utilization of space by each species and which species it might

favour. This competition was considered in relation to its possible importance in influencing dominance relationships between the populations of brown and rainbow trout in Lake Alexandrina. This investigation required consideration of the effects of larger size and prior residence of brown trout, acquired through early emergence, on interactions between the species.

A period of residence in spawning tributaries of some lakes can be advantageous for survival of underyearlings (see review by Northcote 1978). Thus the competitive ability of a species at the underyearling stage in the spawning tributary may be crucial in determining its population dominance status. For example, in Lake Eucumbene (Australia) a decline in the rainbow trout population was attributed mainly to competition from juvenile brown trout (Tilzey 1972). Rainbow trout were forced out of the spawning streams by earlier emerging brown fry and exposed to heavy predation from adult brown trout at the lotic:lentic interface. Apparently juvenile brown trout are capable of excluding juvenile rainbow trout from the small stream environment. However, evidence of competitive exclusion in nature is rare (Wangersky 1978), rather, coexistence of competitors appears to be the rule and competitive exclusion the exception. Studies on naturally sympatric juvenile stream dwelling salmonids (e.g., Hartman 1965 on steelhead trout and coho salmon, and Glova 1978 on cutthroat trout and coho salmon) indicate that their coexistence may depend primarily on differences in their behavioural ecology which result in competing populations partitioning resources (principally spatially) in streams. The small stream environment provides three major types of flowing water habitat: riffles, pools and glides (runs) or intermediate channels (Mundie 1974), in which resources may be partitioned horizontally between habitat types or vertically within the deeper water habitats. Stream salmonids exhibit flexible behaviours permitting opportunistic exploitation of resources.

Larkin (1956) hypothesized that this characteristic is an adaptation to the instability of freshwater environments and is possessed by freshwater fish in general. Consequently freshwater fish are able to utilize a wide variety of food and habitat types. Sympatric populations may exhibit much niche overlap, particularly if resources are plentiful, but when competition becomes more intense a greater degree of niche separation may occur. Niche separation occurs as each population confines its range of resource utilization to those resources to which it is best adapted to utilize or compete for (Nilsson 1956).

Therefore potential competitive interactions between underyearling brown and rainbow trout in the stream environment were investigated in relation to habitat utilization. The importance (or degree of realization) of potential competition between underyearling brown and rainbow trout in Scotts Creek was evaluated by studying their population dynamics and comparative species abundance and was considered in relation to the outcome of competition for spawning space on these components.

Connell (1975) described three general methods used to detect or measure biological interactions (such as competition or predation) under natural conditions: 1/ observations of patterns existing in nature with assessment of their apparent fit to theoretical models, 2/ searching for the "natural experiment" e.g., comparing the niche of a species between locations where a competitor is present and absent (this experimental approach suffers from lack of an adequate control), and 3/ the controlled field experiment, which Connell regards as the preferred approach. In the present study, a combination of field observations and a controlled experiment was used to detect and measure the extent of competition for spawning space, mediated through redd superimposition. Modified field experiments using model stream sections (or stream observation troughs)

were used to investigate the potential for competition for space and the dominance relationships between underyearling brown and rainbow trout. Field observations revealed the probable significance of this potential competition between the underyearling populations in Scotts Creek.

CHAPTER II

STUDY AREA

2.1 INTRODUCTION

Field work was carried out at Lake Alexandrina, located in the Mackenzie Basin of the South Island of New Zealand (Fig. 2.1). The study of competitive interactions between, and juvenile population dynamics of, brown and rainbow trout was carried out in Scotts Creek, the major tributary of Lake Alexandrina.

2.2 LOCATION AND CATCHMENT OF LAKE ALEXANDRINA

Lake Alexandrina is situated 1.6 kilometres southwest of Lake Tekapo in the upper catchment of the Waitaki River (latitude 43°56' South, longitude 170°27' East) at an altitude of 716 m.a.s.l.. It is set in glacial till, which has a slightly subdued morainic topography, and outwash gravel (Gair 1967). More detailed information on the geomorphology of the area is given by Mansergh (1973) and Laird and Lewis (1976). The lake is 7.2 kilometres long and has a mean depth of 13.6 metres and a maximum depth of 27 metres (Irwin 1978). It has a shoreline of 16.8 kilometres and covers an area of 658 hectares (Moore et al. 1962).

Small streams enter the lake on all sides but only three are permanently flowing. At the northern end of the lake the two main inlet tributaries, Scotts Creek and Muddy Creek drain an extensive area of swampland, much of which has been modified and drained as a result of agricultural development. An outlet stream flows eastwards from midway

along the eastern shore into Lake McGregor which in turn drains into Lake Tekapo.

Tussock grasslands (in which Festuca novaezealandiae is dominant), introduced pastoral grasses and weedmats of Hieracium pilosella and H. prealtum clothe most of the catchment. Much of the drier shoreline is dominated by willow (Salix sp.), matagouri (Discaria toumatou) and sweet briar (Rosa rubiginosa) and the marsh areas by raupo (Typha orientalis), and sedges (Carex spp.).

2.3 CLIMATE

The climate in the Upper Waitaki Basin is governed by prevailing wind systems. Characteristically, northwesterlies (fohn type winds) succeed anticyclones as they lose intensity and are terminated with cold front passages (O'Connor 1975). Annual precipitation in the area is about 900mm. Seasonal variation in rainfall is small, ranging from a mean of 148mm in both winter and summer to 154mm in autumn. Snow falls occasionally around Lake Alexandrina in most winters but seldom persists on the ground for any length of time. The Lake Alexandrina locality experiences cold winters and warm summers. Extreme mean daily maximum and minimum air temperatures recorded in the area during the period 1927 to 1974 were -9°C and 28°C, and the mean annual air temperature for the same period was 9°C. The area is characterized by an excellent sunshine regime. An annual mean of 2278 hours of bright sunshine was recorded in the area over the period 1963-1973 (O'Connor 1975). Further information on the climate of the Upper Waitaki area is given by O'Connor (1975).

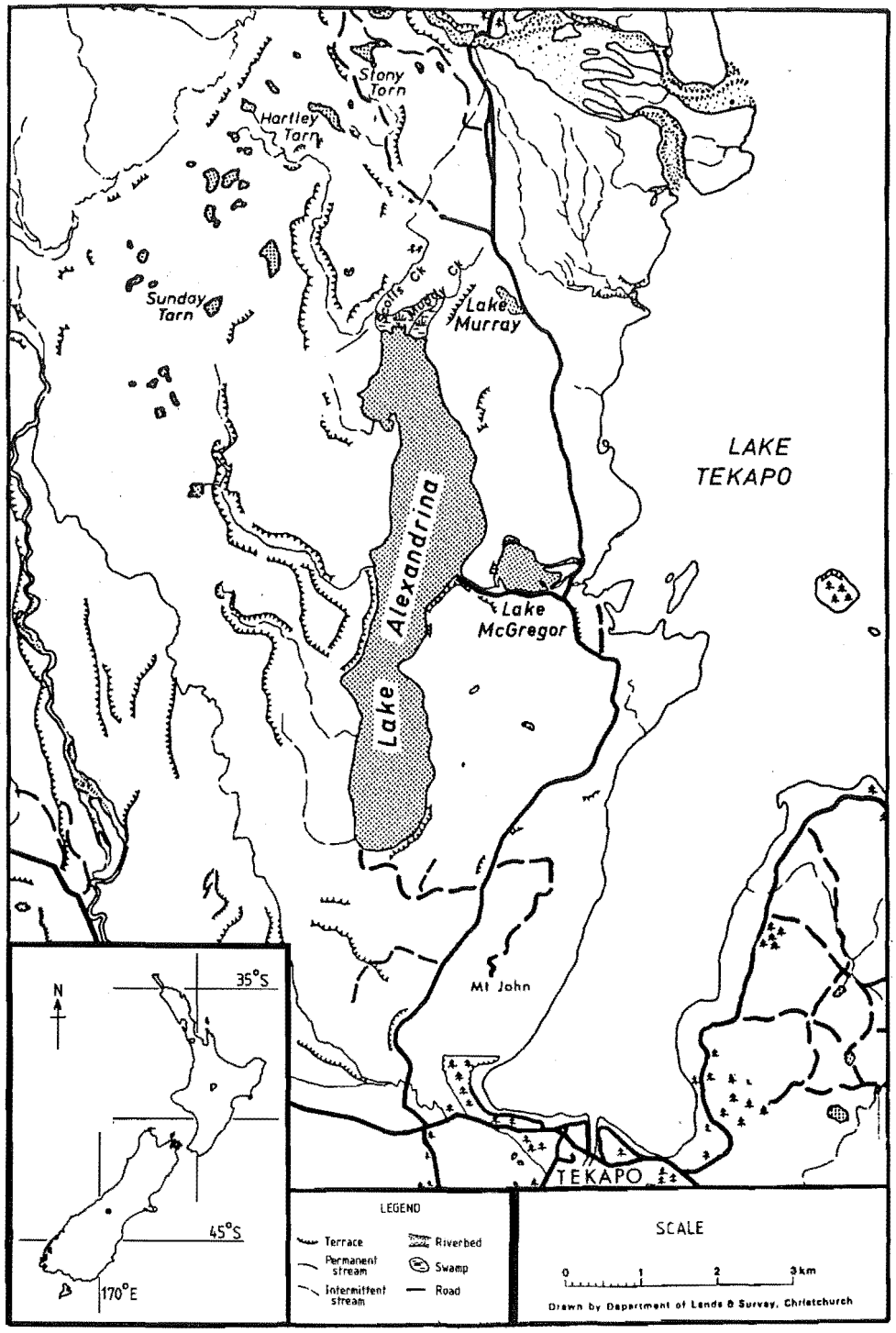


Figure 2.1 The study area. The inset shows the location of Lake Alexandrina in the South Island of New Zealand.

2.4 SCOTTS CREEK

Scotts Creek emerges from a small swamp approximately 1.5 kilometres north of Lake Alexandrina and meanders for most of its length through improved pasture and modified tussock grasslands and wetlands (Fig. 2.2). It is confined by well defined banks which are high in places and frequently overhanging. Tussock and introduced grasses provide good riparian cover for most of the stream's length. During the summer, watercress (Nasturtium sp.) grows profusely in the upper region of the stream above the grill (Fig. 2.2). The stream has a total length of

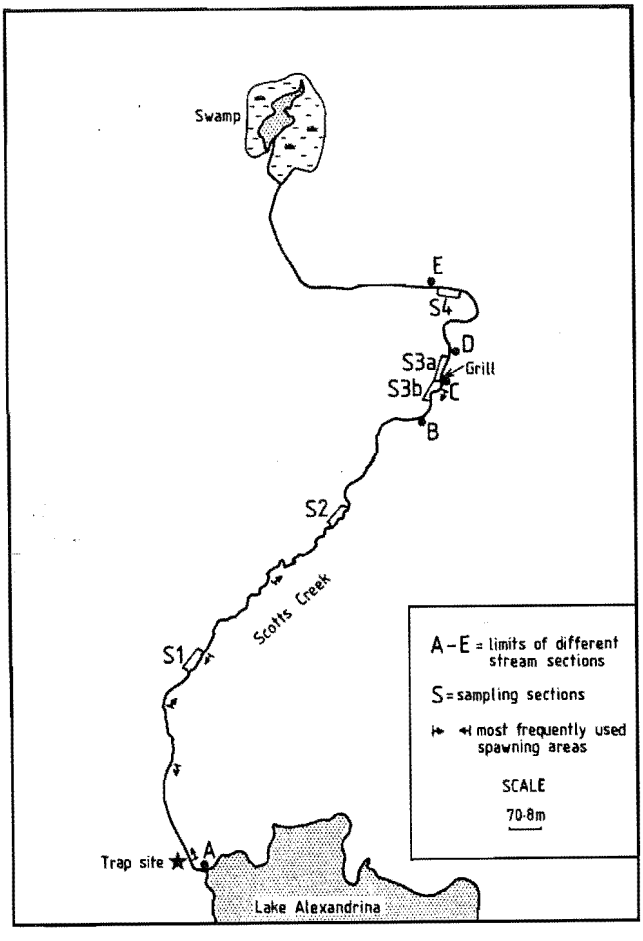


Figure 2.2 Map of Scotts Creek showing the trap site, the electrofishing sampling sections and the most frequently used spawning areas. Drawn from Department of Lands and Survey aerial photograph, 1979 Series.

2.4 kilometres, a mean gradient of 13mkm^{-1} and a mean discharge of approximately 0.125m^{3}s^{-1}. It has a fairly stable flow and is not subject to flooding. Peak discharges are insufficient to cause scouring of bed materials coarser than sand. The stream follows a predominantly riffle:run sequence interspersed by a few pools, and flows over a bed composed of varying amounts of mud, sand and rounded gravels and stones.

Mean water temperatures recorded during the study period ranged from about 13° C during summer to 8° C during winter (Fig. 2.3). Maximum summer water temperatures rarely exceeded 18° C and minimum winter temperatures rarely fell below 5° C.

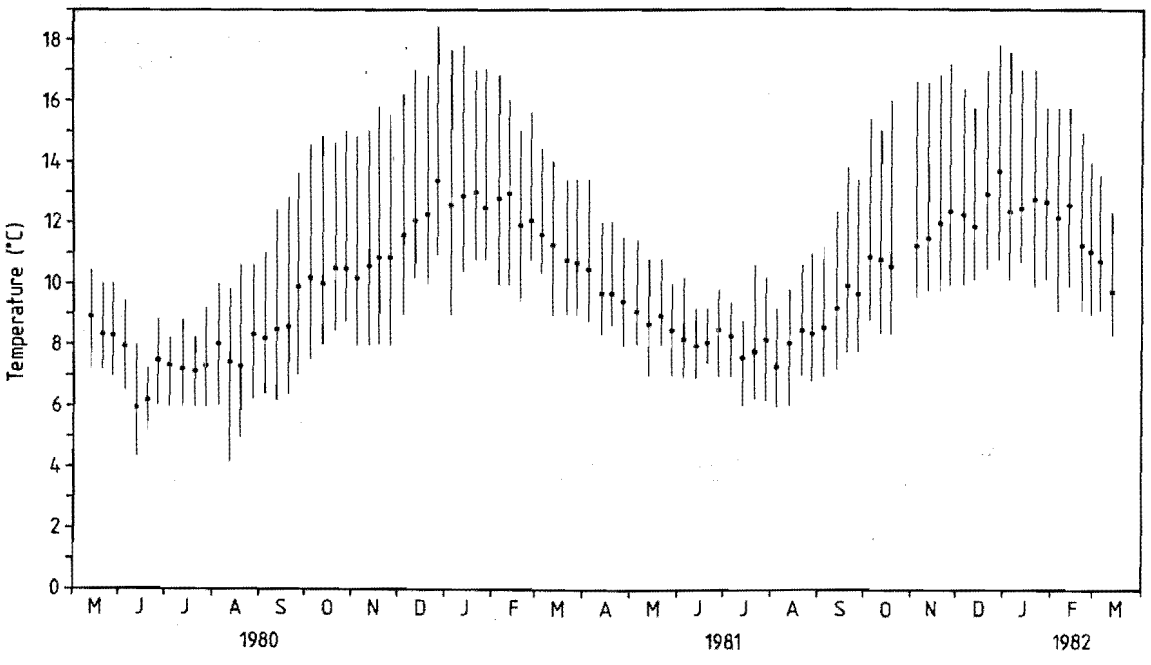


Figure 2.3 Mean weekly water temperature and range in Scotts Creek from May 1980 to March 1982.

Spawning trout usually have access to the 1.5 kilometres of stream immediately above the lake. Access further upstream, where

conditions are mostly unsuitable for spawning, can be prevented by a grill which is usually dropped into position at the start of each spawning season. The better spawning areas, as indicated by the apparent quality of the spawning substrate and frequency of use by spawners, occur within the stretches of stream bounded by arrows in Figure 2.2. Much of the gravel used by spawners has been deposited in the stream by members of the South Canterbury Acclimatization Society in an endeavour to improve spawning conditions.

The underyearling salmonid populations in five sections of the stream (Sections 1,2,3a,3b and 4) were studied over varying periods between 1979 and 1982. These sections were chosen, on the basis of general morphometry and flow characteristics, as being representative of different stretches of the stream. Sections 1 and 2 were considered to represent the stretch between points A and B shown in Figure 2.2 and sections 3a,3b and 4 to represent the stretches between points B and C, C and D, and D and E respectively. Physical characteristics of the stream, including depth, water velocity, flow characteristics, amount of bank overhang and composition of the stream bed were measured in each section (Table 2.1). These characteristics were determined from parallel transects across the stream two metres apart over the length of each section. Water velocities were measured in the middle of the water column with a Gurley Pygmy current meter.

Table 2.1 Physical characteristics of the sections studied. Measurements were made in conditions of average flow.

	SECTIONS				
	1	2	3a	3b	4
Length (m)	50	61	58	51	50
Mean width (m)	2.18 ± 0.12	2.28 ± 0.21	2.88 ± 0.24	1.98 ± 0.14	2.90 ± 0.25
Area (m^2)	109 ± 6	139 ± 13	167 ± 14	101 ± 7	145 ± 13
Mean depth (cm)	30.9 ± 2.39	26.7 ± 3.44	26.2 ± 2.69	34.9 ± 2.25	31.1 ± 2.12
Mean midstream water velocity ($m.s^{-1}$)	0.46 ± 0.029	0.51 ± 0.048	0.46 ± 0.033		0.18 ± 0.024
Flow characteristics - slow (%)	65	38	63	89	100
" " - turbulent (%)	35	62	37	11	0
Bank overhanging >10 cm (%)	15	28	3*		
" " >20 cm (%)	4	38	97*	100 (96*)	100*
Stream bed covering (%)					
mud	13	3	37	27	94
sand	40	20	32	2	
assorted gravels and stones/					
<2.5 cm particle diameter	3	0	6	0	0
<5.0 cm " "	3	8	22	18	0
<7.5 cm " "	11	51	3	28	6
<10.0 cm " "	19	15	0	25	0
10 cm < rocks < 12.5 cm diameter	6	2	0	0.5	0
rocks > 12.5 cm "	5	1	0.1	0	0

* mostly vegetation overhang

CHAPTER III

GENERAL SAMPLING PROGRAMME AND METHODS

3.1 ADULT UPSTREAM MIGRANTS

Information on size and timing of the spawning runs of brown and rainbow trout in Scotts Creek was obtained from daily totals of upstream migrants caught in a fish trap at the stream mouth. The trap was of conventional design, consisting of two fences in a V configuration leading fish upstream into a holding pen. Initially, it was made entirely of wire netting supported by steel standards (Plate 3.1), but later was modified to minimize debris accumulation by substituting vertical wooden slats for wire netting in the holding pen.

The trap was operated continuously from 5 May 1980 until 15 October 1980, except for a three day period in late August when it was sealed and adult fish were denied access to the stream. In the following season, the trap was operated continuously from 9 April 1981 until 18 June 1981. Then it was operated for periods of one week at approximately monthly intervals until October, with the aim of establishing the approximate timing of that seasons rainbow trout spawning run.

The trap was attended at least once daily and records were taken of the species, sex, length (cm) and weight (kg) of each fish caught. Fish were then released and allowed to continue upstream. At regular intervals spent fish returning downstream were herded with hand held wire netting screens, penned and manhandled over the trap to allow their escape back into the lake.

Plate 3.1 Adult fish trap and fry trap in position near the mouth of Scotts Creek.

3.2 OUTMIGRANT UNDERYEARLINGS

Fence traps of the design used by Armstrong and Argue (1977) were used to trap juvenile downstream migrants. Traps were plywood and stainless steel screen installations built across the stream. Downstream migrants were directed by the screens into a sluice trough which emptied into a plywood live box (Plate 3.1). When in operation, the traps were cleared at least twice daily depending on debris accumulation.

Outmigrant underyearlings (progeny of 1980 spawners) were trapped near the stream mouth continuously from the onset of emergence in early August 1980 until 18 June 1981. The following spring, the trap was operated sporadically to establish the approximate form and timing of the 1981 emergence period.

Daily totals of outmigrants usually were obtained from direct counts, but when large numbers of emergent fry (i.e., more than approximately 3000 fry per night) were caught, totals were estimated by volume subsampling.

Monthly mean lengths (mm) of outmigrant fry were estimated from pooled weekly samples.

3.3 RESIDENT UNDERYEARLINGS

Population and growth rate estimates of underyearlings in the stream were made once a month from November to April inclusive for three consecutive years (1979-1980 to 1981-1982). In 1981 an additional estimate was made in June. Population estimates for the stream were calculated by extrapolating population estimates made for the representative stream sections (described in Section 2.4) regularly sampled each summer, to the total area of the stream. Not all of the five stream sections were sampled each year. Sections 1,2,3a and 4 were sampled regularly during the summer of 1979-1980, whereas Sections 1,2 and 3b were sampled during the following two summers. Total length of the stream sampled each year (i.e., 219 metres in 1979-1980 and 162 metres in 1980-1981 and 1981-1982) was greater than one tenth the length of the spawning ground.

Estimates of populations within sections were made by the removal method (Zippin 1958). Each section was isolated with stainless steel mesh screens abutted against permanent bedlogs at either end of the section. The section was then electrofished at least three times in an upstream direction with a 150-630 Volt pulsating D.C. fish shocker. Stunned fish were collected with dip nets and held in live boxes until

sampling was completed. When decreasing catches were not achieved between successive runs, the pooled total was used as an approximate minimum estimate of the population size. When decreasing catches were achieved in only the latter runs, numbers in previous runs were added to a population estimate calculated by the removal equation (in Zippin 1958) for the number of fish remaining.

All fish captured were anaesthetized with benzocaine (0.003%) and species and fork length (mm) were recorded for each fish. Scale samples (for age determination) were taken from fish suspected of exceeding the length range of age 0^+ fish. When completely recovered fish were returned to the section sampled.

Species biomass was computed from the mean measured fork length converted to mean weight by linear regression. The equation for each species was derived from lengths and weights (gm) of freshly killed fish from samples taken, in the 1979-1980 summer (rainbows), and in the 1979-1980 and 1981-1982 sampling periods (browns).

3.4 ESTIMATION OF ERROR

When the mean of a population parameter was calculated by converting between functionally related variables using the linear equation:

$$Y = a + bX$$

a measure of the reliability of the estimated parameter was obtained by combining the variance due to regression with the variance due to estimating X in the equation:

$$\text{var } \hat{Y} = \text{var } \hat{b} \left(\frac{\text{var } \hat{X}}{n} + \bar{X}^2 \right) + \hat{b}^2 \frac{\text{var } \hat{X}}{n} + \text{var } \hat{a} - 2X \text{ covar}(\hat{b}, \hat{a})$$

where var $\hat{b}$, var $\hat{a}$ and covar($\hat{b}$,$\hat{a}$) are calculated from regression analysis. In this situation a G.M. functional regression was used; recommended by Ricker (1973) as the appropriate regression when both variates are measured with error.

CHAPTER IV

EFFECT OF INTERFERENCE COMPETITION FOR SPAWNING SPACE ON SPAWNING SUCCESS

4.1 INTRODUCTION

In some New Zealand freshwater systems in which brown and rainbow trout occur in sympatry and in which rainbow trout are numerically dominant, dominance by rainbows might be favoured by interspecific interference competition for spawning space, mediated through redd superimposition. Later spawning by rainbow trout gives them the potential to limit brown trout populations by dislodging and destroying their eggs through redd superimposition.

Mortality of embryos due to redd superimposition has been discussed by a number of researchers (e.g., Kuznetsov 1928, Hobbs 1937,1940,1948, Semko 1939,1954, Hanavan and Skud 1954, Gangmark and Bakhala 1960, Mathisen 1962, Helle et al. 1964, Lister and Walker 1966, Reed 1967, Hartman and Galbraith 1970, Helle 1970, Schroder 1973). Some observations have indicated that this form of mortality can be serious. For example, a report made by F.R. Lucas on the O'Malley River, Kodiak Island, Alaska, in 1924 (Gilbert and Rich 1927) stated "the reds (red, or sockeye salmon) were now digging out the humpback (pink salmon) eggs. Behind every rock and in every eddy piles of humpback eggs lay. Within 22 steps the writer counted 12 piles that would average 5 gallons to a pile; and behind a small island about 6 feet in diameter there were more than a 50-gallon barrel full of humpback eggs." Krokhin and Krogius (1933) and Krogius and Korkhin (1948) thought that redd superimposition was one of the most important causes of Kamchatka red salmon egg mortality.

Hobbs (1940) concluded that trout stocks in New Zealand had developed to the point where a considerable portion of redds were superimposed and that redd superimposition had the potential to regulate the density of natural populations.

Although losses due to redd superimposition have been reported for a number of salmonids, very little quantitative work has been published to indicate the magnitude of such losses. The first and most detailed work of this kind was by McNeil (1962) on pink and chum salmon spawning in three coastal Alaskan streams. He gave evidence for a direct relationship between egg loss and density of females spawning: that egg displacement increases as the density of spawning females increases, ultimately reaching a point at which females displace from the spawning bed a number of eggs equal to the number they deposit. His model has gained wide acceptance among Pacific salmon researchers because it explains the inverse relationship between spawner density and spawning efficiency that is frequently observed.

This chapter investigates the hypothesis that superimposition of brown trout redds by rainbow trout severely limits the spawning success (defined as the proportion of eggs deposited surviving to emergence) of brown trout spawning in Scotts Creek, and is a major factor causing dominance of rainbow trout over brown trout in Lake Alexandrina.

The study involved: establishing the comparative use made of the spawning stream by brown and rainbow trout, determining the severity of redd superimposition in terms of frequency of redd site use, estimating loss of embryos due to redd superimposition, comparing overall species spawning success and investigating the influence of time of spawning on spawning success.

4.2 SPAWNING MIGRATIONS

The spawning runs of both brown and rainbow trout into Scotts Creek began in early April and continued for brown trout until July, and for rainbow trout until the middle of October (Figs. 4.1 and 4.2). The adult fish trap was installed on 9 May 1980, by which time 91 rainbow trout (59 males and 32 females) and 22 brown trout (9 males and 13 females) were present already in the stream. Previous observations that season on numbers of spawners and redds indicated that few fish would have spawned and returned to the lake before the trap was installed. In 1980 2932 spawners were trapped entering the stream in; species and sex composition of these fish are given in Table 4.1. Fifteen percent of brown trout were blind, and these were destroyed since they were incapable of spawning.

Table 4.1 Species, numbers and sex composition of upstream migrants passing through the adult fish trap in 1980.

		No.	Sex ratio females:males	Species Totals	Percent of total migrants
Rainbow trout	males	997	1.869	2860	97.5
	females	1863			
Brown trout	males	20	2.100	62	2.1
	females	42			
Quinnat salmon	males	3	2.333	10	0.3
	females	7			

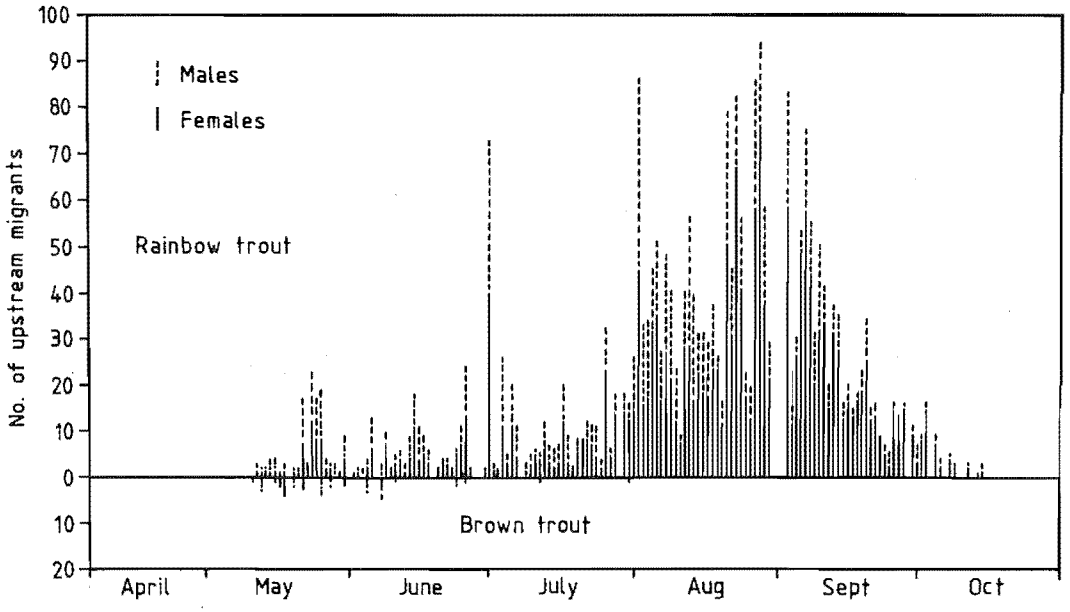


Figure 4.1 Daily number of upstream migrant brown and rainbow trout in 1980. (Number in creek by 10 May; rainbow females (32), males (59), brown females (13), males (9)).

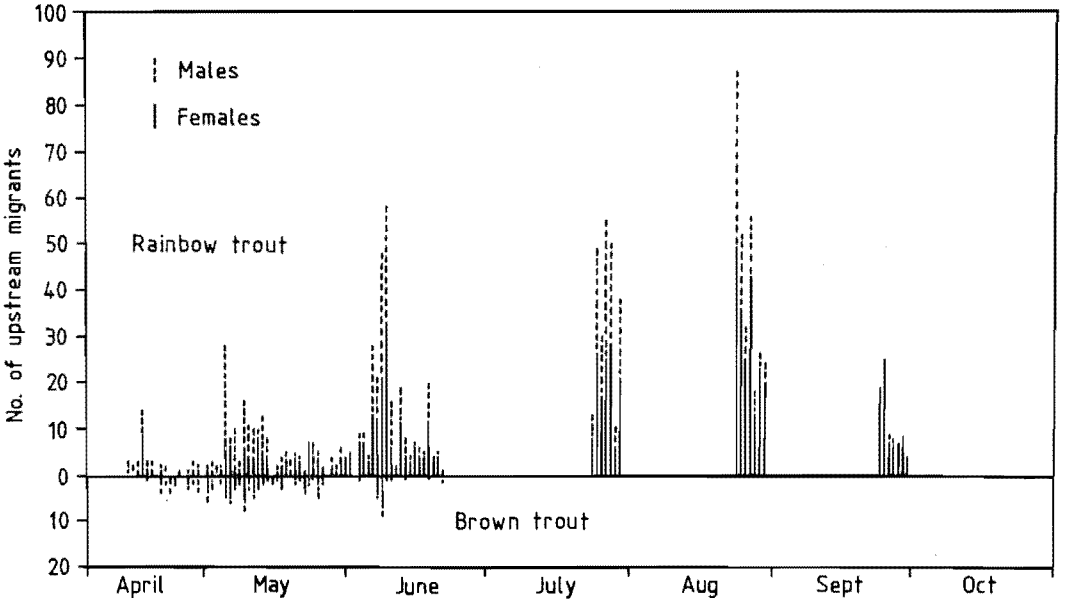


Figure 4.2 Daily number of upstream migrant brown and rainbow trout in 1981.

Over the period of the 1981 spawning season when the trap was operated continuously (i.e., from 9 April to 18 June) 512 rainbow trout, 116 brown trout and 34 quinnat salmon entered the stream to spawn. This was 1.6 times, 1.9 times and 3.4 times more respectively than was recorded over the same period the previous season. However, the form of the rainbow trout run was similar in the two seasons, i.e. there was a pronounced peak late in each season (Figs. 4.1 and 4.2).

In all three species females outnumbered males. Towards the latter half of the rainbow trout run the sex ratio progressively favoured females (Figs. 4.1 and 4.2), whereas very early in the season it favoured males. Female brown trout and salmon occasionally were seen digging redds unaccompanied by males; this may be a consequence of the grossly uneven sex ratios (Table 4.1). On six occasions, possible evidence for mixed spawning between brown and rainbow trout was observed. On four such occasions female brown trout were paired with male rainbow trout, and on two occasions the reverse was seen. Interspecific aggressive interactions between male trout were observed frequently.

Mean lengths and weights of spawners were similar between the two species of trout and between years (Table 4.2). Length distributions of 1980 spawners are shown in Figure 4.3.

Fish usually entered the stream at night. However during peak migration of rainbow trout water temperature may also have been a factor controlling entry into the stream, since regular runs occurred when the stream temperature approached maximum in the early afternoon. Large runs frequently were associated with freshets.

Table 4.2 Mean lengths and weights of 1980 and 1981 spawners.

			n		$\bar{x}$		S.E.	
			1980	1981	1980	1981	1980	1981
LENGTH (cm)	Brown trout	males	20	33	55.0	57.4	1.41	1.34
		females	42	81	55.0	57.8	0.81	0.54
	Rainbow trout	males	995	448	56.0	55.7	0.69	0.25
		females	1843	687	56.0	56.5	0.57	0.16
WEIGHT (Kg)	Brown trout	males	7	33	2.41	2.63	0.144	1.435
		females	22	81	2.82	3.02	0.161	0.079
	Rainbow trout	males	934	238	2.29	2.12	0.018	0.033
		females	1818	274	2.47	2.47	0.012	0.026

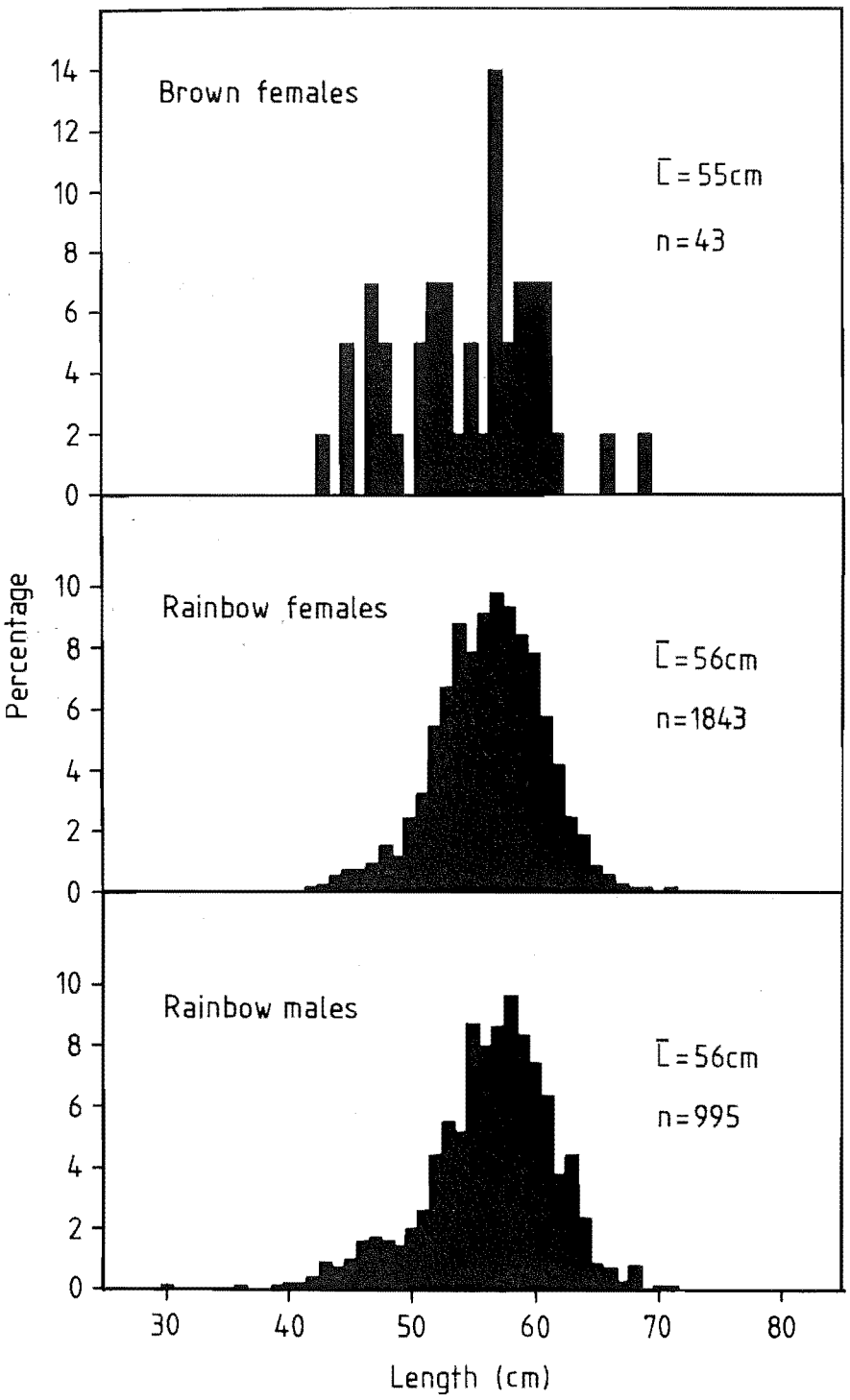


Figure 4.3 Length distributions of upstream migrant brown and rainbow trout 1980.

4.3 SIZE OF THE SPAWNING BED

4.3.1 METHODS

The extent of utilized spawning gravel was divided visually into three categories based on composition of the surface gravel: A - coarse, B - intermediate and C - fine, following Shirazi and Seim (1979). Extent of spawning substrate was described in terms of length rather than area because the stream was too narrow for more than one discrete redd to occur across its width. One to three 10cm-diameter core samples were taken, to a depth of 25cm, from redd sites representative of each category. Each sample was sieved through a geometric progression of sieve sizes from 64mm to 0.063mm. Gravel composition was described by geometric mean particle diameter. Shirazi and Seim (1979) proposed geometric mean particle diameter as the appropriate statistic for characterizing quality of spawning gravel. It is a convenient standard measure which enables comparison of sediment results between studies. It relates to permeability and porosity of sediments and to embryo survival (see Appendix Fig. 3.1) at least as well as percent fines (an ambiguous statistic commonly used in the past), and it is a complete description of total sediment particle composition (Shirazi and Seim 1979).

Geometric mean particle diameter was calculated by the quantile graphical method (Shirazi and Seim 1979) and is given by:

$$d_g = d_{84} \times d_{16}$$

$$\sigma_g = d_{84} / d_{16}$$

where, d_g is geometric mean diameter, σ_g is geometric variance, and d_{84} and d_{16} are the particle diameters at the 84th and 16th

percentiles of the cumulative distribution of particle diameter.

Spatial spawning capacity is described more realistically in terms of individual redd sites available to spawners than in terms of area or length of spawning ground. Number of available redd sites of each grade of substrate was therefore recorded about the time of peak spawner densities when spawning capacity would be approached or exceeded. Redd sites characteristically were mounds of gravel (greater than one square metre) with a mean spacing when contiguous of approximately three metres. This spacing presumably approximates the minimum spacing requirements of females spawning concurrently. Number of redd sites available is equivalent to the maximum number of redds which can be constructed simultaneously.

4.3.2 RESULTS

One and a half kilometres of Scotts Creek is available to spawning fish (i.e., from the mouth to the grill) and of this length approximately 940m is utilized by fish for spawning. Utilized gravel varied greatly in particle composition but broadly could be divided into the three categories (Table 4.3). Full substrate composition and cumulative distribution of particle diameter is given in (Appendices 2.1 and 3.2).

The spawning bed is mostly composed of fine and intermediate gravel types (Table 4.4). Total spatial spawning capacity (in terms of maximum number of redd sites) was approximately 337 redd sites. Eighty to ninety sites (all of A and some of B categories) were greatly favoured; these sites were well endowed with gravel, and mostly were at the heads of riffles or in runs where the stream bed rose in the direction of the flow. Such sites were used repeatedly through the spawning season and

during peak spawning were occupied continuously.

Table 4.3 Geometric mean particle diameter (mm) and variance for samples from substrate categories A, B and C.

	Substrate category					
	A	B			C	
	1	1	2	3	1	2
d_g	23.8	5.4	11.5	20.0	5.5	6.9
σg	2.35	4.64	4.08	3.50	2.01	2.50

Table 4.4 Composition of the spawning bed and number of redd sites.

	Substrate category			Total
	A	B	C	
length (m)	68.5	480.5	391	940
number of redd sites	24	166	147	337

Visual comparisons between preferred, infrequently used, and unused sites revealed an order of preference for physical characteristics correlated with selection of a spawning site. The most important physical

characteristics in order of preference appeared to be bed configuration, substrate particle size, consolidation of the substrate and water velocity.

4.4 FREQUENCY OF REDD SUPERIMPOSITION

4.4.1 METHODS

The frequency with which redds were superimposed during the 1980 spawning season was estimated from maps of successive redds recorded on eight redd sites. Six sites, chosen early in the season, were in locations where a redd had been dug recently on previously undisturbed gravel, and were positioned at fairly regular intervals over the length of the stream. The remaining two sites were chosen later in the season near two of the original sites at which observations had been discontinued. At each site, four aluminium poles were arranged in a rectangle enclosing the initial redd and driven into the banks. Lengths of cord, graduated at 10cm intervals, were suspended between the poles along each bank, and to these a length of nylon monofilament was attached and suspended across the stream. Using the monofilament as a cursor, the distance from the perimeter of the redd to the nearest length of string (i.e., to the nearest side of the rectangle) was measured at 10cm intervals along the length of the redd. The co-ordinates were then transferred to graph paper and an outline map of the redd was drawn. Sites were observed regularly, usually for the length of the estimated incubation period of the initial redd or until the substrate became unusable; all redds constructed at the site during this period were mapped. Thus for each site a series of superimposed redds was recorded. The redds could be presented successively on transparent paper to

graphically show the frequency, sequence and completeness of the redd superimposition. The area of each redd superimposed once, twice, three times etc. was calculated and expressed as a percentage of the total area.

4.4.2 RESULTS

Frequency of redd superimposition was high throughout the season. At one site eight redds were constructed during one incubation period (Fig. 4.4). A record of redds dug on each site and the proportion of each redd superimposed is given in Appendix 2.2. Of 46 redds observed for more than one month, 89% were superimposed. The mean proportion of redd area superimposed was approximately 65%, and mean frequency at which redds were superimposed was once every 19 (± 4) days.

Digging activity on some sites was so intense that it resulted in displacement of most of the gravel downstream leaving underlying boulders exposed, and rendering the site unusable. Observations made over three spawning seasons indicate that such intense digging activity was common and caused continual changes in stream bed topography.

General observations showed that once a redd had been dug on a site there appeared to be a greater likelihood of re-digging in that location i.e., redds appeared to be contagiously distributed. This was particularly obvious late in the season when previously unused sites were heavily utilized once an initial redd was dug. McNeil (1967) demonstrated that pink salmon redds were contagiously distributed in an experimental spawning channel.

Rate of redd superimposition would be expected to increase as spawner density increased. Although general observations supported this view, results from the regularly observed redd sites did not i.e., there

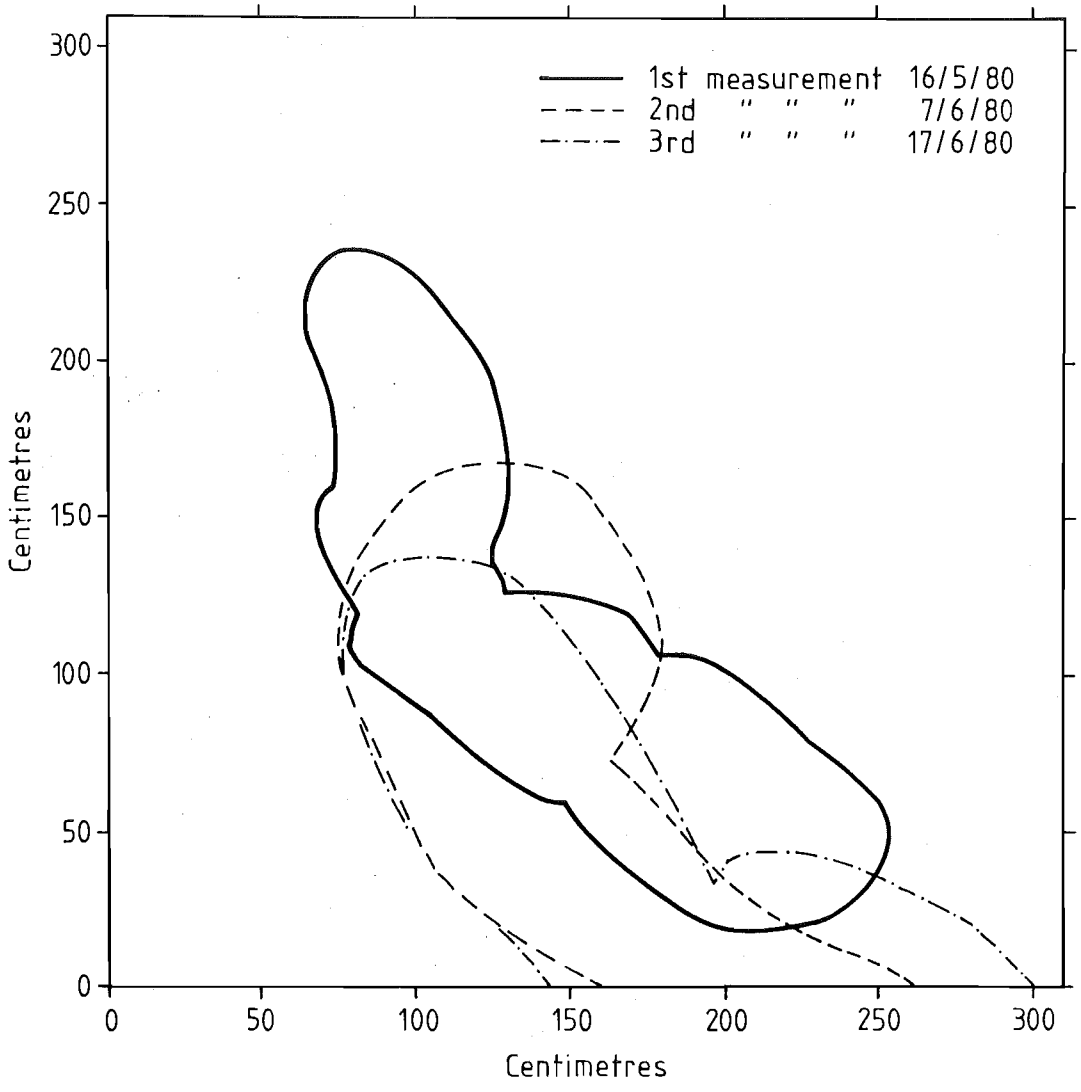


Figure 4.4 Graphical representation of redd superimposition at site 3a.

was no obvious trend in frequency of redd superimposition on any site. However, since site attractiveness continually changes through digging activity of fish altering the configuration of the stream bed, frequency of redd superimposition at any one site need not necessarily exhibit a general trend.

Time of redd site occupation was variable, ranging from less than one day to four days, but the mode appeared to be about three days.

4.5 FECUNDITY

4.5.1 METHODS

Fecundity, defined here as the number of ripening eggs in a female prior to spawning, was determined for brown and rainbow trout from samples of 17 and 28 females respectively, collected from the fish trap during the 1980 and 1981 spawning seasons. Size range of fish in the samples adequately represented size range observed in the spawning runs. Fork length of each fish was recorded and the ovaries were preserved in Gilson's fluid. Number of eggs in the ovaries was estimated later by volumetric sub-sampling. The relationship between egg number and length of female was then examined.

4.5.2 RESULTS

Egg number and fish length were significantly correlated in female brown trout ($P < 0.01$, $r = 0.851$) (Fig. 4.5), but not in female rainbow trout ($r = 0.229$) (Fig. 4.6). For brown trout the relationship between fecundity (F) and length (L) is given by the G.M. functional

regression:

$$Ln F = 2.823\ Ln L - 2.790$$

For rainbow trout, fecundity was estimated by the mean number of eggs per female which was 5272 (± 416).

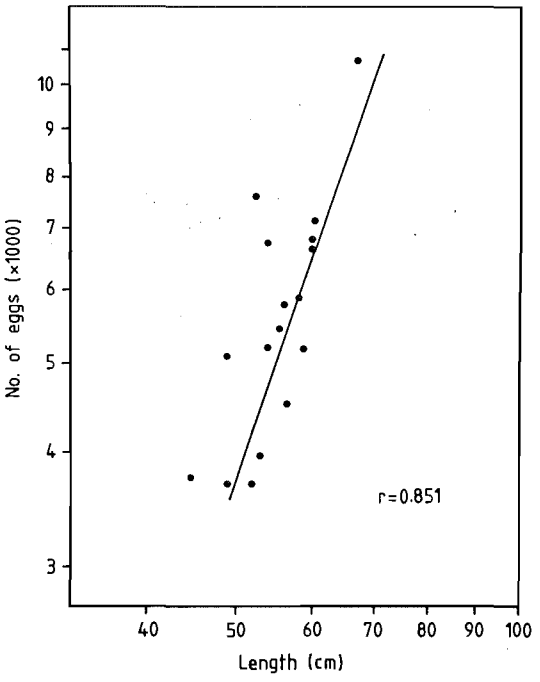


Figure 4.5 Relationship between fecundity and length for brown trout.

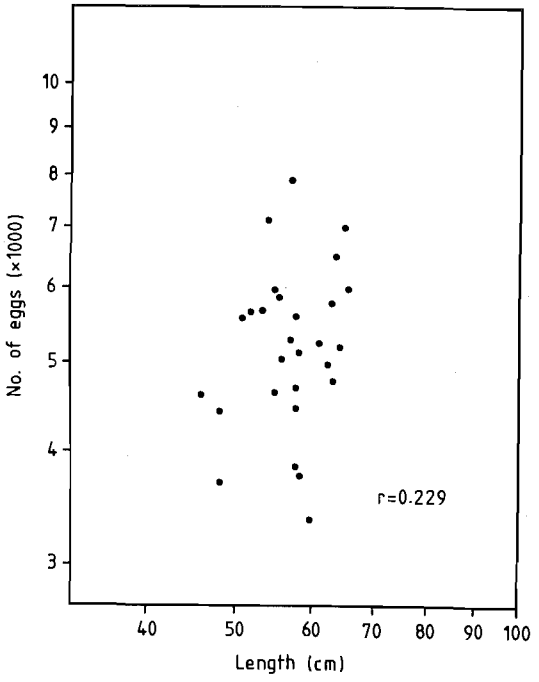


Figure 4.6 Relationship between fecundity and length for rainbow trout.

4.6 SPAWNING SUCCESS

4.6.1 MORTALITY DUE TO REDD SUPERIMPOSITION

4.6.1.1 METHODS

An experiment designed to measure mortality of brown trout eggs and alevins due to redd superimposition by later spawning rainbow trout was carried out during the 1981 spawning season. On 26 April 1981 five female and four male brown trout from the spawning run were placed in each of two contiguous 50 metre sections (1 and 2) of Scotts Creek located immediately below the grill at the upper end of the spawning ground. Spawning substrate in both sections was composed entirely of B (intermediate) grade gravel. The fish were confined within each section (by grills placed at either end) until they had completed spawning. On 14 May the spent fish were removed and the redds in the lower section (Section 2) were exposed to superimposition by later spawning rainbow trout. The downstream grill on Section 2 was replaced with an adult fish trap which was operated continuously until 16 June. This ensured that only rainbow trout entered Section 2. During this period regular mapping of the brown trout redd sites was carried out to obtain a crude estimate of the severity of any redd superimposition taking place. The brown trout run was judged to be practically finished by 16 June so the trap was removed and fish were allowed unrestricted access to Section 2 to spawn. I allowed for an incubation period (i.e., the period from time of fertilization to time of emergence) of approximately two and three-quarter months. On 23 July, after removing all adults present in Section 2, I installed fence fry traps at the downstream ends of each section, to catch all downstream migrating emergent brown fry. These traps were operated continuously until 2 September, when emergence was

judged to be complete. At this time the populations of brown fry remaining in each section were estimated by electrofishing using the removal method (Zippin 1958).

Spawning success of the two groups of female brown trout was compared, and mortality of eggs and alevins due to redd superimposition was calculated.

4.6.1.2 RESULTS

Female brown trout were of similar size in the two sections (Table 4.5); mean length of each group was approximately 56cm and mean weight 2.8kg.

Table 4.5 Lengths and weights of female brown trout spawning in the experimental sections.

	Section 1		Section 2	
	length (cm)	weight (kg)	length (cm)	weight (kg)
	62.0	3.5	59.5	3.1
	58.0	2.9	52.0	2.2
	55.5	2.7	49.5	2.0
	53.5	2.5	62.0	3.9
	53.0	2.4	56.5	2.9
Mean	56.4	2.8	55.9	2.8

Redds were constructed very soon after fish were released into the sections, although length of time taken to dig a redd was variable. The minimum (and modal) time taken to complete a redd was three days, which was recorded for four females. All fish had completed spawning

within eight days. Each female constructed a single redd. In both sections one redd was partially superimposed, but in each case I considered loss of eggs would have been slight since the superimposition occurred at the downstream edge of the redd and therefore probably missed the egg pockets.

When rainbow trout were allowed entry into Section 2 the brown trout redds were severely superimposed. During the period from 14 May to 16 June, when records were taken regularly, 29 female and 16 male rainbow trout entered the section. By the end of this period a mean of 75% of the area of each brown trout redd had been superimposed (Table 4.6).

Table 4.6 Proportion of the area of each brown trout redd in Section 2 (constructed about 13 May) superimposed during the period 14 May to 16 June 1981.

Redd site	Area (m^2)	Proportion of redd superimposed (%)				Total
		1x	2x	3x	4x	
1	2.853	17	19	14		50
2	2.217	59	37			96
3	1.870	38	11	9	22	80
4	0.631	5	79	16		100
5	2.108	30	6	13		49
Mean						75

On 6 June I found about twenty strongly eyed eggs scattered on the stream bed immediately below a freshly superimposed brown trout redd in Section 2. Considering their fairly advanced stage of development, I think these were probably brown trout embryos.

During the period from 17 June to 23 July spawner densities in

Section 2 must have been fairly high since large congregations of adult rainbow trout (totalling over 50 fish) were observed in the section prior to installation of the fry traps. The original brown trout redds were unrecognizable since the stream bed topography had been altered considerably by digging activity of the rainbow trout.

Total fecundity of each group of brown trout females (Table 4.7) was estimated by summation of individual fecundities calculated from the length fecundity relationship (see pg. 34). To calculate potential egg deposition from total fecundity, I allowed for a 2.5% loss due to egg retention within females, non-fertilization, and non-lodgement of eggs in the substrate (Hobbs 1948).

Table 4.7 Spawning success of female brown trout in each of the experimental sections.

	Section 1	Section 2
Total fecundity (No. of eggs)	$27,246^{+10,499}_{-7,577}$	$26,796^{+10,392}_{-7,486}$
Potential No. of eggs deposited	$26,565^{+10,236}_{-7,388}$	$26,126^{+10,132}_{-7,299}$
No. of free swimming fry	5911	358
Spawning success	$22.3^{+8.5\%}_{-6.2\%}$	$1.4^{+0.5\%}_{-0.4\%}$

From 23 July to 2 September, 5213 and 169 brown fry were trapped in Section 1 and Section 2 respectively. Peak fry emergence occurred between 18 and 30 August (Fig. 4.7). In Section 1 the temporary abatement

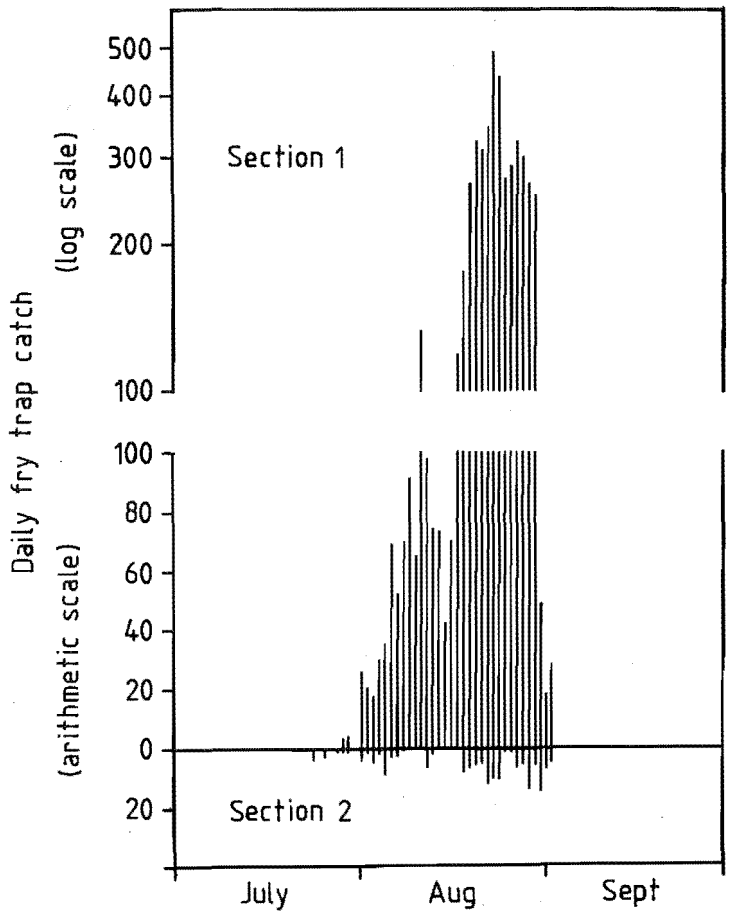


Figure 4.7 Daily catches of brown trout fry caught in fry traps below each of the experimental sections (1 and 2) over the period 23 July to 2 September.

in size of daily catches after the initial minor peak apparently was due to inhibition of emergence and subsequent downstream dispersal in fry caused by nocturnal illumination from the approaching full moon. Full moon occurred on 16 August. Inhibition of downstream dispersal in newly emerged fry by moonlight has been documented for a number of salmonids, for example, rainbow trout (Northcote 1962), coho salmon (Au 1971), and chinook salmon (Reimers 1973 and Unwin 1984). Emergence was judged to be finished by 2 September since by that time most of the catch was composed of fry larger than 30mm, i.e., fry exhibiting evidence of a period of stream growth. Mean length of fry trapped during the emergence period was 27.4 (± 0.1)mm. The population of brown fry remaining in Section 1 and

in Section 2 on 2 September was 698 and 189 respectively, and the mean lengths of these fish were 29.2 (± 0.3)mm and 29.0 (± 0.5)mm.

Spawning success (i.e., the quotient of number of free swimming fry divided by potential number of eggs deposited) was much lower in Section 2 than in Section 1 (Table 4.7). Values for spawning success shown in Table 4.7 are minimum estimates because mortality of free swimming fry in the experimental sections was not taken into consideration. In the absence of redd superimposition there was only 22.3% survival of eggs, from fertilization to emergence. Loss of eggs through redd superimposition in Section 2 is given by:

$$\%\ \text{loss of eggs through redd superimposition} = \frac{\text{potential No. free swimming fry} - \text{observed No. free swimming fry}}{\text{potential No. free swimming fry}}$$

where potential number of free swimming fry is calculated from potential number of eggs deposited, given 22.3% survival of undisturbed eggs in the gravel. It is assumed that mortality of free swimming fry was similar between each section. I thus calculated that approximately 94% of eggs and alevins in Section 2 were lost through redd superimposition (Table 4.8).

Table 4.8 Calculation of loss of brown trout embryos in Section 2 due to redd superimposition by rainbow trout.

Potential No. of eggs deposited	.....	$26,126 \begin{smallmatrix}+ 10,132 \\ - 7,299\end{smallmatrix}$
Potential No. of free swimming fry	.. $26,126 \begin{smallmatrix}+ 10,132 \\ - 7,299\end{smallmatrix} \times 0.223 \begin{smallmatrix}+ 0.085 \\ - 0.062\end{smallmatrix}$	$= 5,826 \begin{smallmatrix}+ 5,350 \\ - 2,802\end{smallmatrix}$
No. of free swimming fry recorded	.....	358
% loss due to redd superimposition	..... $\dfrac{5,826 \begin{smallmatrix}+ 5,350 \\ - 2,802\end{smallmatrix} - 358}{5,826 \begin{smallmatrix}+ 5,350 \\ - 2,802\end{smallmatrix}}$	$= 93.9 \begin{smallmatrix}+ 2.9\% \\ - 5.7\%\end{smallmatrix}$

4.6.2 SURVIVAL OF EGGS IN UNDISTURBED REDDS

4.6.2.1 METHODS

In addition to estimating survival of eggs from fertilization to emergence in undisturbed redds in experimental Section 1 (Section 4.6.1.2), I also got an indication of embryo survival from six redds constructed on 7 May 1980. It is not known to which species of trout these redds belonged. An estimate of mortality was obtained from the ratio of dead to total eggs and alevins collected from redds (Hobbs 1937). A serious deficiency in this technique is that it does not account for eggs that were buried and subsequently disappeared from redds. In Scotts Creek the major cause of egg disappearance is by redd superimposition, and so to overcome this problem I protected the redds

from physical disturbance by covering them with coarse wire netting. On 4 July 1980 the redds were carefully excavated with a shovel to a depth of approximately 50cm, and when eggs were discovered the redd material was thrown up into the current which caused the lighter eggs and alevins to be carried into a 1mm mesh bag net anchored immediately downstream from the redd. The numbers of dead and live eggs and alevins were counted. Substrate analysis was not carried out on these redds. I visually estimated that they covered the range of gravel compositions from A (coarse) to C (fine), but no attempt was made to correlate mortality with gravel composition.

4.6.2.2 RESULTS

Estimates for survival of eggs in undisturbed redds were variable (Table 4.9). The mean of 33% (± 15%) compares favourably with

Table 4.9 Survival estimates for undisturbed eggs in the gravel determined by excavation of protected redds.

Redd No.	No. of eggs dead	No. of eggs alive	No. of alevins dead	No. of alevins alive	Total No. of eggs + alevins dead	Total No. of eggs + alevins alive	% survival
1	445	609	0	4	445	613	58
2	99	14	0	1	99	15	12
3	51	13	0	0	51	13	20
4	234	0	72	58	306	58	16
5	286	179	7	18	293	197	40
6	640	601	70	169	710	770	52
						Mean	33 ± 15%

the estimate of 22.3% determined for survival of undisturbed brown trout eggs (Section 4.6.1 2), considering that the former did not cover the full period of incubation and therefore would overestimate actual survival.

4.6.3 OVERALL SPAWNING SUCCESS

The potential population fecundities (i.e., total number of eggs in all females) of brown and rainbow trout in the 1980 spawning season were 187,340 (+92,242/-61,812) and 9,753,200 (± 769,600) (95% confidence limits) eggs respectively. These were estimated by multiplying the expected fecundity of an average size female (5,510 (+2,713/-1,818)) in the case of brown trout, or the mean number of eggs per female (5272) in the case of rainbow trout, by the total number of spawning females (34 for brown trout and 1,850 for rainbow trout). Number of females spawning was slightly less than the number recorded entering the trap because some were removed for fecundity analysis, and because of debility. The expected fecundity of an average sized female brown trout was obtained from the length fecundity regression. Pitcher and MacDonald (1973) showed that the usual logarithmic transformation of fecundity on length gives an underestimate which increases with the regression coefficient and the length range. However, according to Figure 1 in Pitcher and MacDonald (1973), which they recommend for determination of the magnitude of this error, the above fecundity estimate underestimates the true value by no more than one percent.

Allowing for 2.5% loss of eggs due to egg retention, non-fertilization and non-lodgement, I estimated potential egg depositions of 182,657 (+89,936/-60,267) and 9,509,370 (± 750,360) eggs respectively for brown and rainbow trout. At high spawner densities egg

retention has been shown to increase (Schroder 1973); therefore the above estimate may be too low, particularly for rainbow trout spawning during the peak spawning period.

Total fry output from redds in 1980 was estimated for each species by combining resident population estimates determined as close to the end of emergence as possible, with the number of underyearlings caught in the fry trap up until that time. These will be minimum estimates since mortality of migrant and resident fry are not accounted for.

For rainbow trout, emergence was judged to be finished by about 1 January 1981. The resident 0^+ rainbow trout population on 1 January was approximately 20,500 fish, estimated by extrapolating the 1980-1981 0^+ rainbow trout survivorship curve back to that date (see Fig. 5.4). By 1 January 1981, 182,323 underyearling rainbow trout had been caught in the fry trap; combining this figure with the resident population estimate gave a minimum estimate of 202,823 rainbow fry for the 1980 season.

Brown trout fry emergence was judged to be finished by about 12 September 1980. Sample sizes of brown trout taken by electrofishing were too small to enable a survivorship curve to be drawn for this species, so the population estimate made on 13 November 1980 (i.e., the earliest electrofishing population estimate) was used as the closest available approximation to the population of 0^+ trout at the end of emergence. It was estimated that approximately 319 0^+ brown trout were in the stream on 13 November, and 120 had been caught in the fry trap by that time. Summation of these totals gave a minimum estimate for brown trout fry output for the 1980 season of 439 fry.

Using the estimates of potential egg deposition and of resulting fry output, I calculated that overall spawning success of brown trout and of rainbow trout in 1980 was approximately 0.2 (± 0.1)% and 2.1

(+0.2/-0.1)% respectively.

4.6.4 RELATION OF SPAWNING SUCCESS TO TIME OF SPAWNING

When redd superimposition is an important factor limiting spawning success, time of spawning is critical in determining the degree of success a female will experience. Late spawners should have higher mean spawning success than early spawners, since their eggs will have a lower probability of being disturbed by subsequent spawners. This difference would explain why rainbow trout, most of which spawn later than brown trout, had an overall spawning success an order of magnitude greater than brown trout.

To test the above hypothesis further, I compared the relative spawning success of rainbow trout whose progeny emerged during three selected portions of the emergence period. It was assumed that numbers of emergent fry (fry smaller than 30mm) caught in the fry trap were consistently proportional to numbers of fry emerging in the stream. The portions selected were: from the onset of emergence to the beginning of peak emergence (i.e., prior to 27 October), during peak fry emergence (i.e., 27 October to 1 January), and from the day of peak fry emergence to the end of emergence (i.e., 26 November to 1 January). The periods of egg deposition from which these groups of fry originated were determined by back calculating incubation times (from emergence) to fertilization (Appendix 1). These egg deposition periods were determined to be: from the onset of spawning to 15 August, which corresponds with the section of emergence prior to the beginning of peak emergence; from 15 August to the end of spawning, which corresponds with the section of emergence during the peak period; and from 14 September to the end of spawning, which corresponds with the section of emergence from the day of peak emergence

to the end of emergence.

Number of females arriving on the spawning ground during each of the selected spawning periods was used to calculate egg deposition during each period. It was assumed that number of arrivals approximated number of spawners. A comparative measure of spawning success was then calculated for fish spawning in each period, using the estimated number of eggs deposited and the number of emergent fry trapped during each corresponding section of the emergence period.

Late rainbow spawners did indeed have higher spawning success than early spawners; spawning success increased from 0.2% to 10.5% (Table 4.10 and Fig. 4.8). The most successful fish spawned sometime after 14 September.

4.7 DISCUSSION

4.7.1 GENERAL

In Scotts Creek, both brown trout and large numbers of rainbow trout spawn on a very limited spawning bed. Severe interference competition for spawning space, mediated through destruction of eggs by redd superimposition, occurred between the species and also within the rainbow trout stock, favouring late spawners. Size and timing of the spawning runs determined the intensity of competition for spawning space, and which species was favoured.

The spawning runs of both brown and rainbow trout began in early April and continued, for brown trout, until July, and for rainbow trout, until the middle of October with a pronounced peak occurring in late August and early September. Numbers of rainbow trout spawners far

Table 4.10 Comparative spawning success of female rainbow trout spawning during three periods of the 1980 spawning season.

Spawning Period	No. of females arriving on the spawning ground	Estimated No. of eggs deposited	Corresponding emergence period	No. of emergent fry trapped	Comparative spawning success (%)
Onset of spawning to 15 August	722	3,711,224	Onset of emergence to 27 October	7,644	0.2
15 August to end of spawning	1105	5,679,921	27 October to end of emergence	175,856	3.1
14 September to end of spawning	233	1,197,667	26 November to end of emergence	125,784	10.5

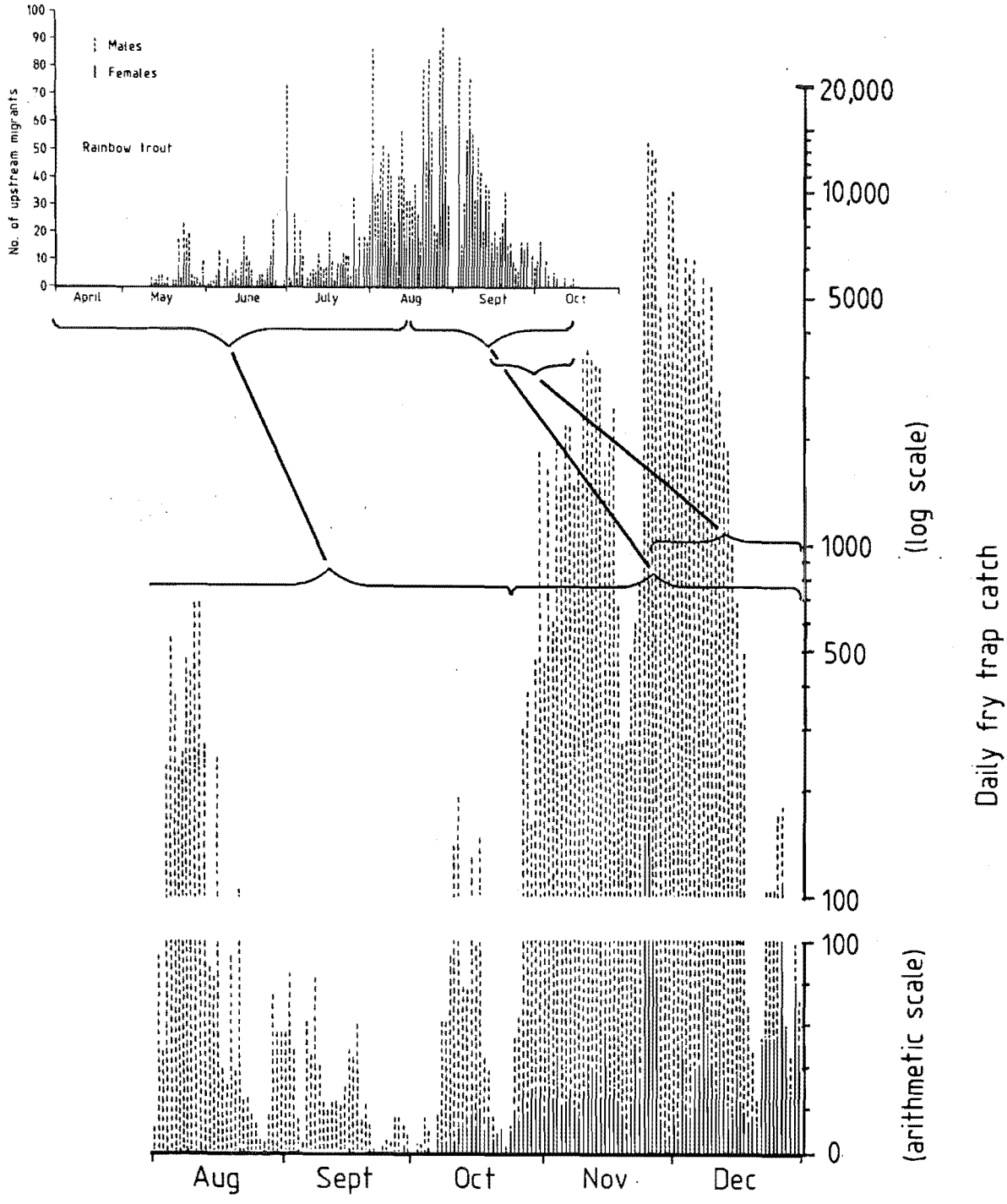


Figure 4.8 Comparison between number of adult rainbow trout arriving on the spawning ground and the number of their emergent progeny caught in the fry trap for three periods of the spawning season.

exceeded those of brown trout; for example in 1980 the total spawner ratio was 46:1 in favour of rainbow trout. Timing and distribution of the 1980 and 1981 spawning runs were similar and, given the stability of the system, I consider they are typical of spawning runs currently occurring in Scotts Creek. Observations of the spawning runs made over a number of years by South Canterbury Acclimatization Society field staff support this view.

The ultimate factor limiting spawning success of trout populations utilizing Scotts Creek is size of the spawning bed. Only 940 metres of the stream is used for spawning and the narrow bed allows room for no more than one discrete redd across its width. Total spawning capacity is approximately 337 redd sites. Three-hundred and ninety-one metres of the spawning bed (the equivalent of 147 redd sites) could be described as marginal spawning substrate, which would probably contribute little to total fry output. This substrate (grade C) had a small geometric mean particle diameter (5.5mm to 6.9mm) and low geometric variance (2.01 to 2.50) i.e., it was composed mainly of fine particles including a large proportion of fine sediments. Fisheries researchers generally agree that excess fine sediments in the spawning gravel of salmonids cause embryo and larval mortality (Iwamoto et al. 1978). According to Shirazi and Seim (1979), embryo survival in grade C gravel should be low (Appendix 3.1).

In fact, embryo survival in grade C gravel, and indeed in all three substrate categories, will be lower than that predicted by Shirazi and Seims' correlation between percent survival and geometric mean particle diameter, for the following reason. Core samples were taken from redds during peak rainbow trout spawning, in late August. The spawning gravel by this time, had been cleaned (i.e., much of the fine material removed) by the digging activity of females. Thus the proportions of fine particles would have been at their lowest levels and would be expected to

increase by sedimentation during the incubation period once spawning activity ceased. The estimate of incubation survival of 22%, obtained from Section 1 in the experiment on the effect of redd superimposition on brown trout spawning success, agrees with the above hypothesis. According to Shirazi and Seim's figure (Appendix 3.1), a geometric mean particle diameter of 11.5mm (obtained from spawning substrate in Section 1) should correlate with an incubation survival of approximately 50%. Brown trout in the experiment were however, spawning in virgin gravel, which was noticeably silty. Consequently the geometric mean particle diameter and related embryo survival at that time was probably lower than that recorded later at peak rainbow trout spawning when the gravel had been well cleaned.

The intermediate grade of spawning substrate (B) had the highest geometric variance and was the most difficult to assess visually. Cleaning of fine materials from the substrate surface produced a visual impression of greater apparent coarseness than was the case for the whole substrate. Grade B encompassed a wider range of substrate composition than A and C, and it overlapped with C (Table 4.3). Thus a proportion of gravel assessed as B would in fact have been marginal spawning substrate. This reduces the number of productive redd sites (i.e., those that contribute to the bulk of fry output) to less than 190 (sum of A and B grade redd sites).

Spawning females preferred some sites over others, and these were always in A and B substrate categories. Preferred use of spawning sites by trout has been reported by other researchers (e.g., Hobbs 1937,1940, McNeil 1967, Hartman and Galbraith 1970), and simply reflects selection by trout of sites possessing particular physical characteristics. Cues that fish apparently can use in selecting a site are : the presence of gravel, usually in the range 2.0cm to 6.5cm, with low silt load and slightly consolidated (Hobbs 1940); gradient of the

stream bed, rising in the direction of the flow (Hobbs 1940); depth and water velocity (dependent on size of fish (Milner et al. 1981); accelerating water velocity (White 1942); ground water seepage (Benson 1953, Hansen 1975); and downward movement of stream water into the gravel (Stuart 1953, 1954). Some of these cues are interdependent, for example accelerating water velocity usually occurs where the bed is rising in the direction of the flow. Selection is not always precise and fish may spawn in less suitable marginal sites (Hobbs 1937, White 1942), particularly if overcrowding occurs on the better sites (Peterson 1978, and personal observations). In Scotts Creek the most important physical characteristics in order of preference appeared to be bed configuration, particle size, consolidation and water velocity. The order of preference is influenced by the range of each physical characteristic available. For example, because of its small size, Scotts Creek did not provide a wide range of depth and water velocities, hence fish were forced to spawn in depths and water velocities they might not normally utilize if a wider choice was available. Under conditions of intense crowding the range of conditions available to individual fish is reduced further.

In Scotts Creek, small size of the spawning bed and limited number of preferred sites led to a very high frequency of redd superimposition, particularly on preferred sites, and this was aggravated further by contagious distribution of redds. Presumably, contagious distribution of redds arises because the construction of a redd favourably modifies the physical conditions for spawning on that site, thereby making it more attractive to later spawners. This was particularly obvious in some marginal and initially unused sites which appeared to have all the prerequisites for spawning except a favourable gradient i.e., the bed fell slightly in the direction of the flow. If a redd was constructed on such a site the bed assumed a rising tendency and thereafter frequency of redd superimposition increased. Similarly

attractiveness of some sites appeared to increase after consolidated gravel was loosened by previous spawning activity.

The sex ratio of spawners in both species greatly favoured females. Numerical dominance by females in spawning runs of trout, usually in repeat spawners, has been reported by a number of authors (e.g., Hobbs 1937, Mottley 1938, Shapovalov and Taft 1954, Ball and Cope 1961, Kwain 1971 and Hunt 1972). Higher spawning mortality in males might be responsible for the imbalance in sex ratio. Males can serve more than one female, and consequently can be exposed to prolonged physical exertion. Mottley (1938) showed that males experience a greater body tissue weight loss than females at spawning. Even though the female loses a greater percentage of her total body weight during spawning (mainly through release of eggs), it is the male which must draw on a greater store of food reserves in order to survive this period. This apparently results in higher post-spawning mortality in males than in females. In addition, Boreman (1981) presented evidence indicating that male rainbow trout are more vulnerable than females to angling.

The rainbow trout runs in Scotts Creek were dominated by males early in the season and progressively by more females later in the season. Since females greatly outnumbered males in the brown trout spawning run, an excess of male rainbow trout present at the same time might have encouraged interspecific spawning. Correct mate pairing may be hindered further by the long, narrow nature of the stream which would serve to visually isolate individuals. Evidence of interspecific spawning was observed but not all cases involved female brown trout pairing with male rainbow trout. Artificial hybridization of brown and rainbow trout has been successful (e.g. Hofer 1909, Stokell 1949, Buss and Wright 1956, Suzuki and Fukuda 1971, Blanc and Chevassus 1979). The most successful cross appears to be rainbow females with brown males. However, survival potential of the alevins is poor. For example, Blanc and Chevassus (1979)

obtained hybrid alevins from rainbow female x brown male crosses which had reasonably good survival up to the 15th day after hatching but poor survival subsequent to that stage. The reciprocal cross produced a few embryos which never hatched. It cannot be presumed, on the basis of success in artificial hybridization experiments, that natural hybridization between these species is possible. I have never seen trout from Lake Alexandrina that, visually, could be described as hybrids. However, it is difficult to identify salmonid hybrids from morphological or anatomical characters because of phenotypic variability in the parental species (Suzuki and Fukuda 1973). Observations of mixed pairs of spawners on redds is not evidence that interspecific spawning actually takes place. In accordance with my observations of solitary females digging redds, Hobbs (1937) considered that the presence of a male is not necessary to stimulate the female into preparing a redd, but is necessary to induce oviposition. It is possible that different courtship patterns would prevent oviposition in mixed species pairs. However, if such an isolating mechanism does not exist it is likely that the result of hybridization would be scarcely noticeable, given the high mortality of hybrids at the egg and and alevin stage (Alm 1955). Thus, the end result of interspecific spawning would be to lower the spawning success of each species. In Lake Alexandrina, this would affect the brown trout population most since it is the smaller of the two and hence would suffer proportionately greater loss.

4.7.2 ASSESSMENT OF LOSS IN REDDS

Many workers have reported the occurrence of redd superimposition but few have been able to estimate losses of embryos resulting from it. Hobbs (1937, 1940, 1948) discussed in detail the

occurrence of redd superimposition in New Zealand and speculated that losses were fairly extensive, possibly averaging 30%. Some researchers have presented indirect evidence of loss due to redd superimposition, for example, Krogius and Krokhin (1948) and Krogius (1951) attributed extremely poor spawning success to redd superimposition by later spawners when runs of sockeye salmon were large and the spawning period prolonged. McNeil (1962) quantified mortality of pink and chum salmon embryos due to redd superimposition by comparing expected density of eggs in the spawning bed (i.e., potential egg deposition) with observed density of eggs in the spawning bed shortly after spawning. He described an asymptotic relationship between density of female spawners and those depositing their eggs safely, from which he estimated mortality from redd superimposition at 25% at the highest observed density of 4.5 spawners per $100ft^2$ ($30.48m^2$). Hartman and Galbraith (1970) reporting on the Gerard rainbow trout spawning stock in the Lardeu River, Canada, found approximately 26% of 217 redds were superimposed, and that about 239,000 eggs were displaced through redd superimposition and failure to lodge in the gravel after spawning, but they did not include the proportion of eggs deposited that this number represented. In the experimental spawning section of Scotts Creek, approximately 94% of embryos were lost through redd superimposition. It is possible that upstream migrating adults may have accumulated below the barrier in the experimental spawning section (Section 2), possibly resulting in higher digging activity and consequently higher frequency of redd superimposition than in the rest of the stream. Such a disparity in frequency of redd superimposition would be greatest early in the spawning season, before the stream's capacity for spawning space was exceeded. Eggs deposited in the experimental spawning section and in the rest of the stream would eventually have been subject to similar disturbance from redd superimposition, but eggs in the experimental section might have been disturbed at an earlier stage of

development since capacity for spawning space in that section might have been exceeded earlier in the season. Egg mortality due to mechanical shock is highest in early stages of development (i.e., to the appearance of eye pigmentation) (Smirnov 1960), hence losses due to this aspect of redd superimposition may have been greater in the experimental spawning section than in the rest of the stream. However, losses due to dislodgement of eggs eventually would have reached similar levels (i.e., maximum levels) within and outside the experimental section as overall spawner density increased later in the season. Another factor which might have caused overestimation of losses due to redd superimposition is violation of the assumption that mortality of free swimming fry before capture was equal in the two experimental spawning sections. Because of the much higher fry output, predator (mainly yearling salmonids) saturation was more likely to have occurred in Section 1 than in Section 2. This would have resulted in a proportionally higher loss of fry in Section 2 than in Section 1, which in tern would cause overestimation of mortality due to redd superimposition. In conclusion, I consider that the estimate of mortality due to redd superimposition obtained from the experimental spawning sections should be regarded as a maximum loss but it was probably representative of losses occurring in the most preferred spawning sites, since such sites were heavily utilized throughout the season.

Narrowness of the spawning bed promoted complete rather than partial redd superimposition. Thus losses due to redd superimposition were probably higher in Scotts Creek than in wider spawning beds with similar spawner densities.

Redd superimposition can cause direct or indirect mortality of embryos. Direct mortality results from disturbance of embryos through mechanical shock. In addition, dislodged embryos are subject to damage from exposure to light and are very vulnerable to predation from fish and

birds. In the latter half of the spawning season eggs, mostly dead, were seen drifting over the stream bed continually and collected on the screens of the fry trap. They were frequently encountered, sometimes in large numbers, in the stomachs of spent adults and juveniles. Relodgement of dislodged embryos is possible, but their survival is probably low since they may eventually die from causes mentioned above and, due to their shallow burial, would very easily be dislodged again.

Redd superimposition could indirectly cause mortality by reducing the oxygen supply to embryos when water percolation through an existing redd is reduced by siltation or redirection of flow resulting from construction of contiguous redds. In Scotts Creek, siltation has the greater potential for causing mortality of embyros in existing redds since the gravel contains a high proportion of fine materials. Embryos deposited very late in the spawning season are least likely to be affected by "biological" causes of siltation (i.e., those resulting from digging activity of spawners) since there will be few subsequent spawners, or by "physical" causes (i.e., natural hydrological siltation) because higher water temperatures reduce incubation times.

High digging activity of females throughout the spawning season appeared to improve the quality of the spawning bed by removing fine particles and organic detritus. This would have been most beneficial to the progeny of late spawners. McNeil (1962) recorded a significant decrease in percentage of fine particles in a pink and chum salmon spawning bed in association with spawning. He estimated that spawning females increased permeability of the surface 15cm layer by about two fold. McNeil suggested that: "health problems might arise in a spawning bed over-crowded with eggs. With over-crowding the health of embryos might be endangered by an associated increase in the abundance of pathogenic agents or a decline in quality of intragravel water. Reduction of water quality might be caused by removal of dissolved oxygen and

addition of toxic metabolites by embryos. It is conceivable that removal of eggs by redd superimposition is a necessary mechanism for inhibiting later and possibly more serious mortality resulting from over-crowding".

Survival of salmonid embryos from deposition to emergence is extremely variable among species and within species (Appendix 2.3). The low survival of chum, pink and sockeye salmon occurred mostly in years of high spawner density and was attributed to loss of embryos through redd superimposition. Redd superimposition was undoubtedly responsible for the extremely low embryo survival recorded for brown trout (0.2%) and for rainbow trout (2.1%) in the present study. Values for spawning success will be underestimated in the present study since estimates of fry output were not corrected for mortalities of resident and migrant fry. Also it is possible that crowding of spawners may have caused a greater loss than that allowed for due to egg retention by females.

4.7.3 INFLUENCE OF TIME OF SPAWNING ON SPAWNING SUCCESS

It has been shown that late spawners have higher spawning success and that fry output from brown trout and early spawning rainbow trout redds was very low. In 1980, fish spawning after 14 September (well after peak arrival of adults) produced the bulk of fry output (Fig. 4.8).

In calculating comparative spawning success of females spawning during selected periods of the spawning season, I have made two assumptions: 1/ that numbers of migrant emergent fry were consistently proportional to numbers of fry emerging, and therefore can be used as a comparative indicator of spawning success, and 2/ that number of females arriving on the spawning ground during each selected spawning period approximated the number of females spawning. If the first assumption was violated it most likely would be due to higher rates of downstream

dispersal by later than by earlier emerging fry, perhaps caused by increasing competition for rearing space. Because of the magnitude of the difference between numbers of early emerging and late emerging fry (Table 4.10), such a violation would be significant only if the actual number of early emerging fry was considerably greater than that indicated by newly emerged migrants. However, the low density of resident fry observed in early November (see Chapter V, Section 5.2.4) was consistent with the low level of early fry emergence predicted from the small number of migrants, and indicated that the first assumption was valid. The second assumption should be valid for comparison between the two major spawning periods selected i.e., before and after 15 August. These periods were long and numbers of fish arriving within them were large. Therefore some degree of flexibility in the assumption could be tolerated without incurring significant errors in percent spawning success. However, the same could not be said of the third selected spawning period, i.e., after 14 September. The estimate of comparative spawning success for this period would therefore have been subject to proportionately more error than the others. There is also indirect evidence that the second assumption may well be violated by delayed spawning late in the spawning season. This hypothesis will be considered in the following discussion, in which I examine the spawning dynamics of the system with the aid of simple models.

4.7.4 SPAWNING DYNAMICS

According to the spawning model of McNeil (1962), if density of female spawners, in limited spawning systems, equals or exceeds available spawning space, most of the eggs deposited by previous spawners will be lost. Apparently this situation occurred in Scotts Creek in 1980, judging

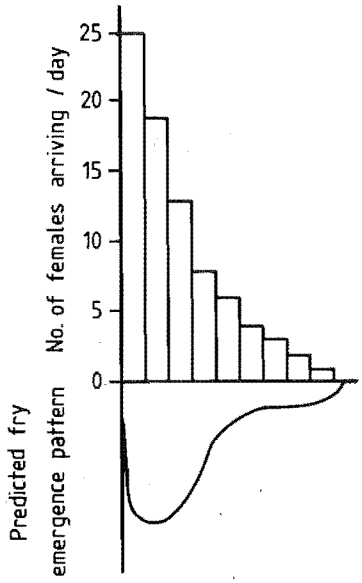
by the low spawning success of early spawners. If density of spawning females merely equals space available, then as the spawning run and rate of redd superimposition declines there will be a proportional increase in numbers of newly deposited eggs escaping displacement and surviving to emergence. Numbers of such eggs will approach a maximum which corresponds with the future peak fry emergence. Thereafter ever decreasing numbers of new eggs will be deposited that will produce the declining phase of fry emergence. In such a system the size of peak fry emergence (or alternatively, peak deposition of eggs surviving to emergence) and the speed at which it is attained, is determined by the capacity of the spawning bed and by the rate at which the run declines. When this model is used to generate a fry emergence pattern for a simplified spawning run, based on the arrival pattern of females in the latter part of the 1980 rainbow trout spawning run, a relatively broad peak, and very drawn out declining phase of emergence is predicted (Fig. 4.9). However, this does not agree with the observed pattern i.e., a large narrow peak in emergence. Increasing water temperatures might be expected to synchronize emergence times thereby compressing the emergence peak. In Scotts Creek this phenomenon can account for a compression of the peak fry emergence period by eleven days (i.e., by 17%). This conclusion was reached after comparing predicted incubation periods determined solely on water temperatures occurring at the time of fertilization with those based on the observed temperature regime occurring over the incubation period. Fry may also possess intrinsic mechanisms for synchronizing emergence, but I would expect these to be effective only over short time periods (see Chapter V, Section 5.3.1).

There is indirect evidence to suggest that much of the spread in the observed peak fry emergence period of rainbow trout could be attributed to natural variation in incubation times of eggs deposited at about the same point in time. This evidence arises from the similarity in

pattern and spread of the above mentioned peak emergence period with that recorded for brown trout spawning in Section 1 (Fig. 4.7). Figure 4.7 shows an example of fry emergence resulting from eggs deposited about the same time (i.e., within one week of each other). The only difference between the spread of this emergence period and that of the rainbow trout peak fry emergence period is that the latter is twice as long in its declining phase of fry emergence. Therefore, according to this evidence, as much as 96% of fry output in 1980 originated from eggs deposited within a short time period (possibly within one to two weeks) more than two to three weeks after peak arrival of females (according to the predicted time of peak deposition of eggs surviving to emergence (Fig. 4.8)).

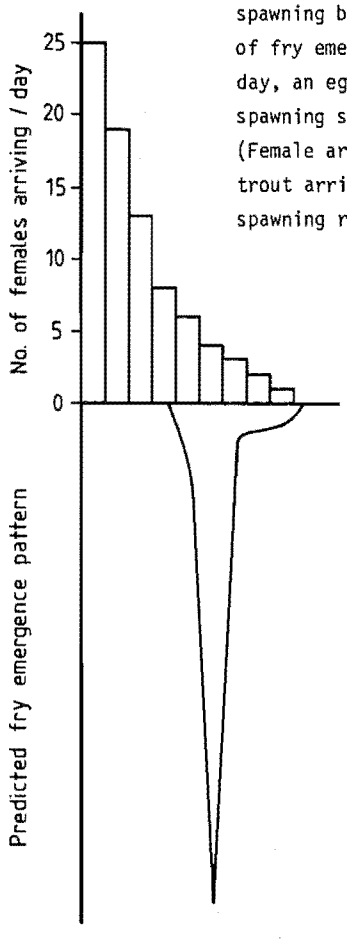
To explain the observed emergence pattern of rainbow fry, it is postulated that during peak spawning newly arriving females delayed spawning and accumulated on the spawning ground. Delay in spawning was possibly caused by the density of female spawners considerably exceeding the available spawning space. Schroder (1973) showed that an increase in number of days before first redd construction occurred with an increase in density of female chum salmon spawners. Such an accumulation, or backlog, of pre-spawners would have been composed of fish that had arrived on the spawning ground at various times in the immediate past. In the initial declining phase of the spawning run, rate of accumulation of pre-spawning females would decrease whereas rate of diminution of pre-spawners (as females acquired space to spawn) would remain constant. Maximum loss through redd superimposition would be maintained while a backlog of females existed. As the backlog of females diminished and the sum of these females and the number of new arrivals approached the maximum number of redd sites, the backlog would be cleared. The vast majority of eggs deposited at that point in time would escape displacement through redd superimposition and survive to emergence, since

Figure 4.9 Simulation of an arrival pattern of females onto a simplified spawning bed of 25 spawning sites, and the predicted pattern of fry emergence, given a redd site occupation period of one day, an egg deposition of 100 eggs/female, and capacity of spawning space filled but not exceeded.
(Female arrival pattern is based on the observed rainbow trout arrival pattern in the declining phase of the 1980 spawning run).



Day	No. of new arrivals	No. of previously deposited eggs surviving to emergence
1	25	0
2	19	600
3	13	1,200
4	8	1,700
5	6	1,900
6	4	2,100
7	3	2,200
8	2	2,300
9	1	2,400
10	0	2,500

Figure 4.10 Simulation of an arrival pattern of females onto a simplified spawning bed of 25 spawning sites and the predicted pattern of fry emergence, given a redd site occupation period of one day, an egg deposition of 100 eggs/female, and capacity of spawning space initially exceeded by 50 fish.
(Female arrival pattern is based on the observed rainbow trout arrival pattern in the declining phase of the 1980 spawning run).



Day	No. of new arrivals	No. of females waiting to spawn	No. of previously deposited eggs surviving to emergence
1	25	50	0
2	19	44	0
3	13	32	0
4	8	15	0
5	6	0	400
6	4	0	2,100
7	3	0	2,200
8	2	0	2,300
9	1	0	2,400
10	0	0	2,500

the number of new arrivals would have declined to very low levels. A large narrow peak of fry emergence should thus be produced, slightly drawn out in its declining phase due to small additions of eggs from very late spawners. When the above assumptions were incorporated into the simple model tested in Figure 4.9, an emergence pattern similar to that predicted and observed for rainbow trout peak fry emergence was generated (Fig. 4.10).

4.7.5 EGG CAPACITY OF THE SPAWNING BED

McNeil (1962, 1964) showed that egg capacity approaches an asymptotic limit with increasing density of spawners. Given the very high density of spawners and loss of eggs due to redd superimposition, I think it is safe to conclude that in 1980 egg capacity of Scotts Creek was exceeded. Hence, egg capacity can be estimated from fry output during the period of peak fry emergence (Table 4.11), and is approximately 890,255 eggs, equivalent to 173 females spawning safely.

Total number of redd sites available in Scotts Creek was approximately 337. Time of redd site occupation by females, although variable, appeared to be about three days. Given the observed temporal distribution of the 1980 rainbow trout spawning run, 337 redd sites and a three day redd site occupation period, it appears that capacity of spawning space could not have been exceeded at any stage of the spawning period. This is obviously discordant with the mechanism proposed in the preceding sub-section (4.7.4). However, more than 147 of the above sites were marginal (i.e., C grade gravel) and only 80 to 90 sites (all with A and B grade gravels) were preferred. Because of the superior gravel, most fry output would have originated from A and B grade redd sites, and in particular from preferred sites. The attractiveness of preferred sites

Table 4.11 Egg capacity of the Scotts Creek spawning bed.

No. of migrant rainbow fry emerging during the peak emergence period of 1980	175,856
Estimated No. of resident under yearling rainbow trout on 1 January 1981	20,000
Estimated total No. of rainbow fry emerging during the peak emergence period	195,856
No. of eggs deposited to produce the total rainbow fry emergence, given 22% survival in redds	890,255
Equivalent No. of females spawning safely, given a mean egg deposition of 5140 eggs per female*	173

* Mean egg deposition was calculated from estimated mean fecundity (5272 eggs per female) given 2.5% egg retention within females, non-fertilization and non-lodgement of eggs in the substrate.

may cause females to delay spawning in order to deposit their eggs in such sites rather than spawn on marginal ground. Thus a female's spawning behaviour might be influenced by two drives, 1/ to spawn and 2/ to deposit her eggs in a favourable location. Which of these drives would exert the most influence presumably depends on time already spent on the spawning ground; the influence of the drive to spawn would increase the longer a female delays spawning. If this hypothesis is correct, capacity of spawning space in terms of "productive space" would have been exceeded for much of the rainbow trout peak spawning period in 1980.

In summary, it was found that competition for spawning space,

mediated through redd superimposition, severely limited the spawning success of brown trout and early spawning rainbow trout in Scotts Creek. The small number of redd sites in relation to the large number of spawners, the narrow nature of the stream, the extended spawning run exhibited by rainbow trout and their habit of contagiously distributing redds, were all factors that contributed to maximizing losses due to redd superimposition. Late rainbow spawners had highest spawning success. However, loss through redd superimposition did not simply gradually diminish as the run declined. Instead, severe congestion on the spawning ground apparently resulted in maximum loss through redd superimposition being maintained until the run declined to very low levels. This situation caused not only a delay in peak rainbow fry emergence but it also determined the pattern of peak emergence.

CHAPTER V

POPULATION DYNAMICS

5.1 INTRODUCTION

Investigation into the population dynamics of underyearling brown and rainbow trout in Scotts Creek was carried out partly as a requisite for the determination of spawning success of adults (see Chapter IV), but mainly to extend comparative information on the two species in this system into the next stage of their life cycles. Scotts Creek serves not only as a spawning ground for adult brown and rainbow trout in Lake Alexandrina, but also as a primary feeding area for some of their progeny prior to migrating to the lake. The aim of the study was therefore to determine the comparative use made of this rearing ground by the underyearlings of the two species. Unfortunately, low numbers of brown trout reduced the scope for comparison of population parameters between the species. However, the population dynamics of the 0^+ rainbow trout alone were of considerable interest, particularly considering the profound influence which intraspecific competition for spawning space has in determining the underyearling population structure of this species.

Information is presented on the species composition, population changes and growth of underyearlings in Scotts Creek over three summers, and their downstream migration and related dispersal over one year and part of another. Published studies on population dynamics of juvenile salmonids in streams generally concentrate on mortality and growth but, due to the great sampling effort required, they lack quantitative information on movements (e.g., Egglishaw 1967,1970, Egglishaw and Shackley 1977,1980, Hopkins 1970, Kennedy 1982, Kennedy and Strange 1980,

Mortensen 1977a,b,c) . In such studies, effects of movements on observed mortality and growth are merely speculated upon. However in the present study knowledge of the outmigration of underyearlings from the study area was fundamental to the understanding of comparative species utilization of the stream and, in addition, it proved useful in interpreting observed mortality and growth. Fortunately, the low and relatively stable flow rate of Scotts Creek facilitated enumeration of outmigrants by continuous trapping.

Contributions to the study of population dynamics of underyearling salmonids in streams pertinent to the present study include those of Allen (1951) and Hopkins (1970) on brown trout and Hopkins (1981) on chinook salmon in New Zealand, Hartman (1958) on rainbow trout in the U.S.A., Egglishaw (1970) and Egglishaw and Shackley (1977) on brown trout in Scotland, Mortensen (1977a,b) on brown trout in Denmark, and LeCren (1962,1965) covering aspects of density relationships of juvenile salmonids. Studies specifically pertinent to the understanding of migration of underyearling trout include those of Hoar (1958), Northcote (1962), Au (1971), Reimers (1973), Kelso, Northcote and Wehrhahn (1981) and Unwin (1984).

The methods used in this study have been described in Chapter III.

5.2 RESULTS

5.2.1 JUVENILE OUTMIGRATION

The fry emergence periods of brown and rainbow trout in Scotts Creek overlap completely. The emergence period of rainbow fry was characterized by a wide and positively skewed temporal distribution, with

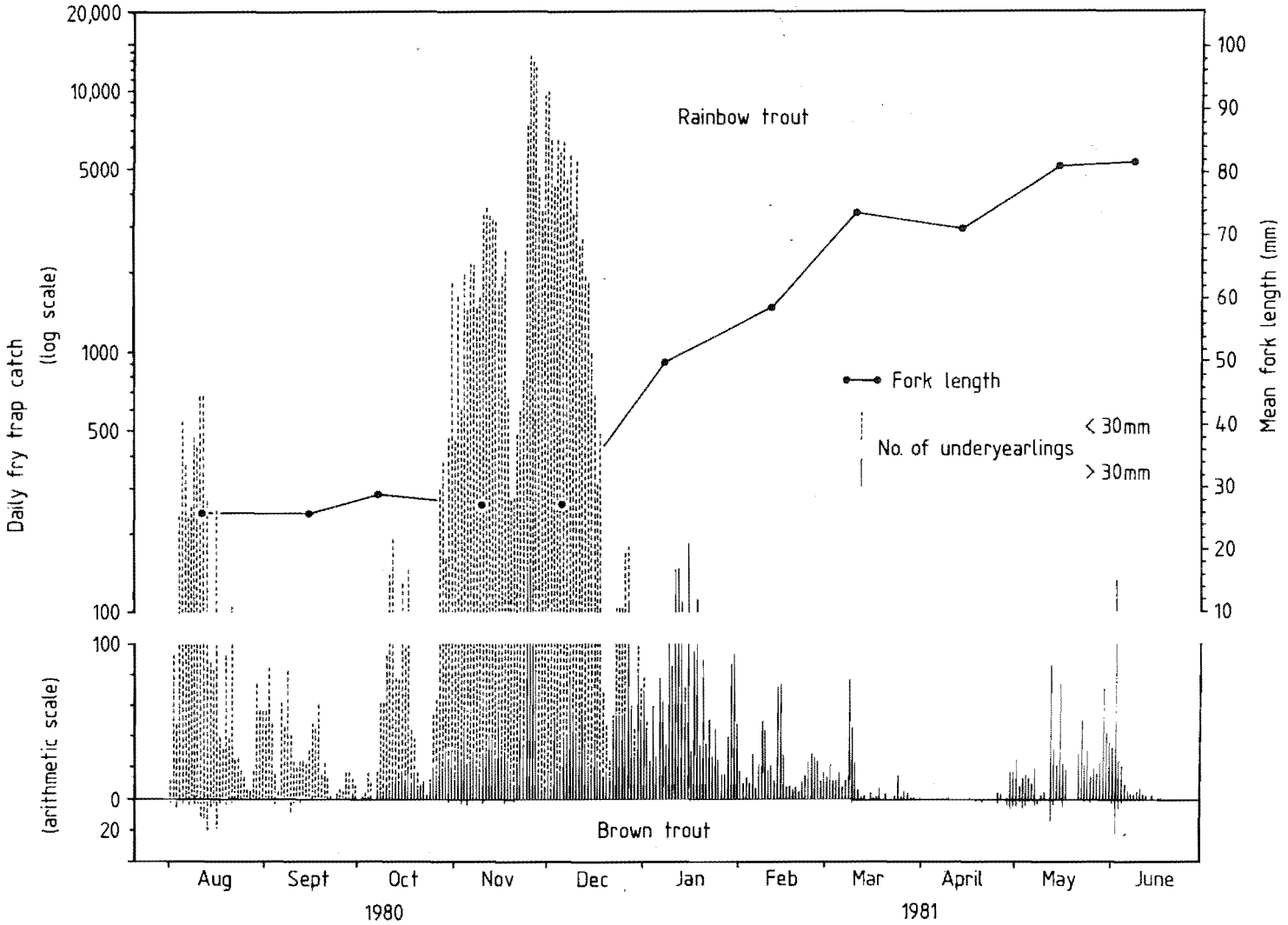
low numbers of fry emerging between late July and late October and with peak emergence occurring in November and early December (Fig. 5.1). The temporal pattern of rainbow trout fry emergence in 1981 (Fig. 5.2) was similar to that of 1980. The emergence period was indicated by large catches of migrant emergent fry (i.e. fish less than 30mm in length) many of which had vestiges of yolk sac visible. Brown fry emerged during late July to late September, but few of this species survived to emergence and the resulting migration of brown fry was insignificant in comparison with that of rainbow fry (Fig. 5.1).

All migration of emergent fry occurred at night and was depressed by moonlight. Usually the majority of fry migrated before midnight, but this pattern was modified by the phase of the moon. When the moon was late in its first quarter it illuminated the stream for the first few hours of darkness, retarding migration of fry during this period. As the moon approached full, the inhibiting effect of moonlight on migration extended further into the night, depressing daily catches of fry, for example during the period 19 to 24 November in (Figure 5.1). As the moon waned in its last quarter, it rose in the eastern horizon progressively later than the onset of darkness. It was during the beginning of this phase that maximum numbers of fry migrated, and they did so during the period of darkness before the moon rose.

General observations on the behaviour of recently emerged fry in still and running water indicated that browns were more closely associated with the substrate and less active in the water column at night than rainbows.

Migration of emergent rainbow fry ceased fairly abruptly in the latter half of December, when emergence of fry ceased. In response to the end of emergence the mean length of migrating fry, which had up until that time been depressed by the large numbers of emergent fry in the catches, rapidly increased due to the larger proportion of post-emergent

Figure 5.1 The brown and rainbow trout underyearling outmigration 1980–1981 and monthly mean lengths of rainbow migrants.



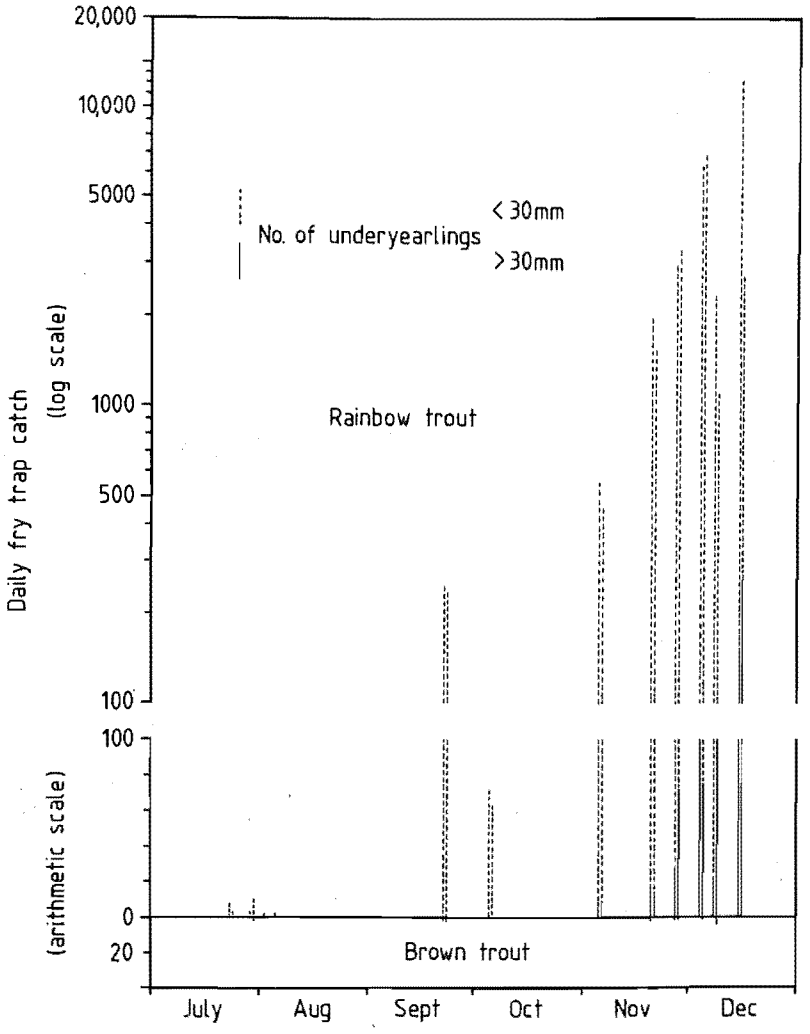


Figure 5.2 The emergent rainbow trout outmigration during selected periods of 1981 indicating the temporal pattern of fry emergence.

underyearlings (i.e., fish which had spent some time living in the stream) in the catches (Fig. 5.1). Migration of post-emergent underyearlings progressively increased from October to January, reached a peak early in January, steadily declined during February and March and essentially stopped for most of April (Fig. 5.1). Few underyearling brown trout migrated during this period; highest numbers were recorded migrating in November, but these were insignificant in comparison with those of rainbow trout. Both species exhibited an outmigration of

fingerlings in the autumn and early winter (i.e., late April to early June), coinciding with the entry of adults into the stream at the beginning of the spawning season. Migration of fingerlings was also mostly nocturnal.

Of the total estimated fry output from the redds in 1980, 439 brown trout and 203,474 rainbow trout, approximately 120 (27%) and 183,474 (90%) respectively migrated to the lake as recently emerged fry. These values were calculated by combining the number of recently emerged fry of each species caught in the fry trap with population estimates determined by electrofishing as close to the end of emergence as possible i.e., 13 November and 1 January for brown and rainbow trout respectively. Total underyearling output from the stream into the lake was 191,631 rainbow trout and 309 brown trout, of which 96% and 39% respectively left as emergent fry.

5.2.2 MARK RECAPTURE OF RECENTLY EMERGED FRY

During the 1980 rainbow fry emergence period I attempted to compare growth and movement of recently emerged rainbow fry emerging at the beginning and end of the peak emergence period. Recently emerged rainbow fry in the upper reaches of the spawning ground were trapped on 22 and 30 November 1980 and on 1 January 1981 and spray marked with green or red fluorescent grit (Phinney, Miller and Dahlberg 1967, and Pribble 1976). In November, the marked fish were released below the upstream trap site about one hour before night-fall on the following evening: but in January, catches were accumulated, marked, and released on the fifth day. Recaptured marked fish were identified using a portable U.V. light viewing box. I planned to recapture these fish in the monthly

electrofishing samples, and in the main fry trap at the mouth of Scotts Creek. However, this experiment was largely unsuccessful due partly to low marking efficiencies (between 27% and 82%) and the associated difficulty in capturing and processing sufficient numbers of fish to ensure a significant recapture rate. Also high mortality and injury of fry caused by the marking procedure contributed to the failure of the experiment. I chose this technique because it is claimed to be a fast method of marking large numbers of fish in the field with a mark that is retained for reasonably long periods of time (up to 5 to 8 months) Rinne and Deacon (1973), Healey, Jordan and Hungar (1976) and apparently is invisible to other fish and predators. However, my results and observations indicate that in the present study retention of marks by fry was low, and mortality and the occurrence of abnormal behaviour in marked fry high. This largely explains the low numbers of fry recaptured (Table 5.1).

The November release was most successful, with 12% of marked fry recaptured, all in the downstream fry trap within 11 days of their release. Seventy-six percent were recaptured within the first two days. The January release was completely unsuccessful; consequently the original aims of the experiment could not be achieved. The main result of this experiment was to show that downstream dispersal of recently emerged fry could be both rapid and extensive, e.g., recently emerged fry were seen to move 1km downstream in one night.

5.2.3 SPECIES COMPOSITION OF RESIDENT JUVENILES

The juvenile salmonid populations in Scotts Creek were dominated by rainbow trout. In all three consecutive summers of sampling, more than 95% of the mean catch per summer was 0^{+} rainbow trout (Table 5.2).

Table 5.1 Numbers of recently emerged fry marked with fluorescent spray recaptured in the fry trap at the mouth of Scotts Creek following release 1 km upstream on 22 and 30 November 1980 and 1 January 1981.

No. marked and released	22/11/80	30/11/80	1/1/81
	846	3630	504
		No. recaptured/day	
Day 1	3	186	
2	16	147	
3	10	48	
4	1	11	
5		25	
6		8	
7		2	
8		4	
9		4	
10		0	
11		1	
15/1/81 Section 2 (electrofishing)		2	
% recaptured	3.5	12.1	0

Table 5.2 Mean number of fish and percentage species composition in electrofishing catches over three summers.

	Mean No. of fish caught		% composition 0^+	1^+	2^+
1979-80	236	rainbow	96.8	0.5	
		brown	2.1	0.2	0.06
		quinnat	0.1		
1980-81	347	rainbow	95.4	1.6	
		brown	3.0	0.1	
		quinnat			
1981-82	390	rainbow	95.2	1.1	
		brown	3.3	0.3	0.04
		quinnat	0.9		

As most fish left the stream as underyearlings, the percent composition of the 1^+ and 2^+ fish was very low. Also, most fish that remained in the creek after the first summer migrated to the lake in the following spring and early summer.

On average, brown trout resided longer in the stream than rainbow trout (Section 5.2.1), resulting in numbers of yearlings of the two species being more similar than those of underyearlings (Tables 5.2 and 5.3).

5.2.4 DENSITY

Analyses of changes in density of underyearlings were carried out only on rainbow trout, since sample sizes of brown trout were small and variable.

In all years the densities of resident early emerging fish were

low. This was most clearly seen in the November 1979 sample which was taken earlier in the month than in the following years, and consequently was not influenced by high numbers of recently emerged fry from the peak rainbow trout emergence period (Table 5.3).

Initial densities of fry were usually higher in downstream sections, 1 and 2 (described on page 12). Recruitment of downstream dispersing emergent fry from upstream reaches of the stream apparently was responsible for this imbalance. However, in December 1981 densities of fry were highest in Section 3b (the uppermost section sampled that summer). I suspect that sampling on that occasion coincided with peak fry emergence in Section 3b, since the great majority of the catch were emergent fry, and this produced temporarily high densities of pre-migrant fry. By the end of the summer growing season (i.e., April) densities of underyearlings were similar throughout the stream below the grill, e.g. in Sections 1,2 and 3 in 1981 and 1982. In the 1979 spawning season, spawners were allowed access to the upstream sections of Scotts Creek, above the grill. However, spawning densities were low and as the quality of the spawning substrate was poor in this area the initial densities of fry in Sections 3a and 4 in 1979-1980 were low.

By January of each year there appeared to be some upstream movement of fingerlings. This was most clearly seen in Section 3a in 1979-1980, when fingerling density increased between December and March (Table 5.3). In the following two seasons, although no spawning took place in this section, and sampling was discontinued there, numbers of fingerlings were observed to increase over the summer.

Initial densities of fry in Scotts Creek were high. The maximum recorded was 7.67 fry.m^{-2} (combined densities of brown and rainbow fry in Section 3b in December 1981). This is not excessively high for stream dwelling salmonid fry, which have been reported in initial densities as

Table 5.3 Monthly densities (fish m^{-2}) in each electrofishing section (see page 11) over three summers.

Month and date of sampling	Section	1979-1980					1980-1981				1981-1982			
		Rainbow		Brown			Rainbow		Brown		Rainbow		Brown	
		0+	1+	0+	1+	2+	0+	1+	0+	1+	0+	1+	0+	1+
November	1	0.39									3.11	0.018	0.018	0.009
3 - 1979	2	0.57		0.036			3.18	0.014	0.158	0.007	4.21	0.129	0.079	0.014
13 - 1980	3a/3b	0.20					3.42	0.030	0.010	0.010	1.19	0.139	0.248*	0.030
15 - 1981	4	—	—	—	—	—								
December	1	4.22					5.33				7.45		0.009	
10 - 1979	2	5.73	0.007	0.043			5.40	0.007	0.151		5.12	0.014	0.093	0.007
11 - 1980	3a/3b	1.68	0.024	0.012	0.012		4.12	0.020	0.020	0.010	7.55		0.119	0.020
16 - 1981	4	0.61	0.035	0.007	0.007	0.007								
January	1	4.69					5.33	0.055	0.028	0.009	6.20	0.009	0.055	
16 - 1980	2	4.26	0.007	0.029			4.99		0.129		4.33		0.079	
15 - 1981	3a/3b	1.82	0.018	0.012		0.006	2.04	0.010	0.139		4.01		0.089	0.040
18 - 1982	4	0.53	0.007	0.028	0.007									
February	1	2.47					4.54		0.018					
14 - 1980	2	2.90	0.007	0.036	0.007		4.17	0.022	0.086					
12 - 1981	3a/3b	1.70		0.018			2.26	0.040	0.079	0.010				
	4	1.05		0.090	0.007									
March	1	2.75		0.009			2.59	0.009	0.037		1.83		0.046	
12 - 1980	2	2.53	0.014	0.014	0.014		3.04	0.014	0.058		3.44		0.065	0.007
16 - 1981	3a/3b	2.13	0.012	0.042			1.45	0.069	0.069		1.75	0.010	0.129	
17 - 1982	4	0.55		0.021	0.007									
April	1	2.20					1.90				1.24		0.037	
11 - 1980	2	2.45					2.32				1.77		0.007	
15 - 1981	3a/3b	1.08					1.85				1.56		0.020	0.010
16 - 1982	4	0.37												
June	1						0.38							
16 - 1981	2						0.31							

Section 3a was sampled during 1979-1980 whereas
Section 3b was sampled during 1980-81 and 1981-1982.

* This higher density of 0+ brown trout resulted from the experimental protection of brown trout redds (Chapter IV, Section 4.6.1).

high as 10 fry.m^{-2} (LeCren 1965) and 18.1 fry.m^{-2} (Mortensen 1977c) for brown trout, 10 fry.m^{-2} (Egglishaw and Shackley 1977) for brown trout and Atlantic salmon combined, and 65 fry.m^{-2} (Hopkins 1981) for quinnat salmon. The above authors found that the rate of loss of fish during the first growing season was related to initial population density, suggesting that mortality was density dependent. I investigated the possibility of density dependent mortality occurring in the Scotts Creek underyearling rainbow trout populations by comparing combined mean monthly densities in Sections 1 and 2 from January to April in 1980 and 1982 (Fig. 5.3). I used January rather than December density estimates as starting densities since they immediately followed the end of emergence and, unlike the December estimates, were reliable for all three years.

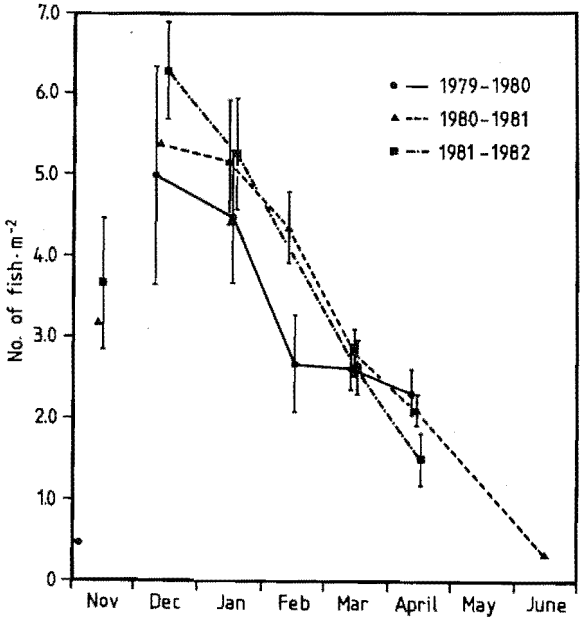


Figure 5.3 Combined monthly mean densities (90% confidence limits) of underyearling rainbow trout in electrofishing sections 1 and 2 over three summers.

Instantaneous rate of loss M, of each population, during this period was calculated according to the formula:

$$M = (ln N_1 - ln N_2) / (t_2 - t_1)$$

Where N_1 is the number (or density) of fish present at the beginning of the period at t_1 days and N_2 is the number present at the end of the period at t_2 days. Although higher rates of loss were associated with higher January densities (Table 5.4), the differences were slight, and since there were also few data points, regression analysis revealed no significant relationship between the two variables. In addition,

Table 5.4 Comparison of January density with instantaneous mortality rate (M) over the period January to April using combined mean monthly density estimates for the years 1980-1982.

	January density	M
1980	4.48	0.015
1981	5.17	0.020
1982	5.27	0.028

confidence limits for all three January estimates and for two of the April estimates overlapped. Hence differences in densities between years can be explained by error in density estimation. Perhaps clearer evidence for density dependent loss can be seen by comparing December and April rainbow trout densities between Sections 1 and 2 in 1981-1982 (Table 5.3). In this example, the higher initial density in Section 1 rapidly

declined to a level similar to that in Section 2 by April. In previous years the densities in the two sections had been more similar throughout the summer, indicating that they had similar carrying capacities (Table 5.3).

5.2.5 POPULATION SIZE AND MORTALITY OF 0^+ RAINBOW TROUT

5.2.5.1 METHOD OF POPULATION ESTIMATION

From the monthly density estimates for each sampling section, I calculated monthly population estimates of 0^+ rainbow trout for the entire stream. However, rather than applying the mean monthly density of all sampling sections to the entire area of the stream, I applied the densities obtained for each section to areas of the stream I considered they most accurately represented, and then summed the populations in each area. In all years, populations present between points A and B (see Figure 2.2) were estimated using mean densities for Sections 1 and 2 combined. During most of the 1979-1980 summer the populations between points B and D and between points D and E were determined using the densities from Sections 3a and 4 respectively. However, in November 1979 the population between D and E could not be estimated since sampling was not carried out in Section 4 that month. I consider that exclusion of this portion of the population would not seriously effect the total population estimate since fry densities in that area were generally low. In 1980 and 1981 spawning did not occur above the grill and therefore the method of estimating underyearling populations above point B was modified. For all of the sampling period the population between B and C was determined from densities in Section 3b, and from January onwards allowance was made for upstream migration of fingerlings above the grill

by including an additional estimate for the area between C and D using densities from Section 3b. In June 1981 only Sections 1 and 2 were electrofished, so an estimate of the density of underyearlings in Section 3b was calculated by:

$$J_{3b} = J_{1,2} \, (A_{3b} \, / \, A_{1,2})$$

where J_{3b} and A_{3b} are the densities in Section 3b in June and April respectively, and $J_{1,2}$ and $A_{1,2}$ are the combined mean densities in Section 1 and 2 in June and April.

5.2.5.2 RESULTS

Monthly population estimates were used to construct survival curves for the three summers (Fig. 5.4). For each year, observed losses in numbers of fish during the period January to April were approximated by a negative exponential relationship of the form:

$$N = a \, e^{-Zt}$$

where N is the number of fish in the population at time t, and a and Z are constants. Z is commonly known as the instantaneous mortality rate. For the 1980, 1981 and 1982 survival curves a is 10.1519, 10.5134 and 10.8960 respectively and Z is 0.0070, 0.0097 and 0.0135. I extrapolated these curves back to 1 January, i.e., to about the end of emergence. Further extrapolation would incur significant error in population estimation, because prior to this date recruitment of fry into the population was continuous and the emigration rate of such fry was higher, and their mortality was also likely to be higher, than older fry.

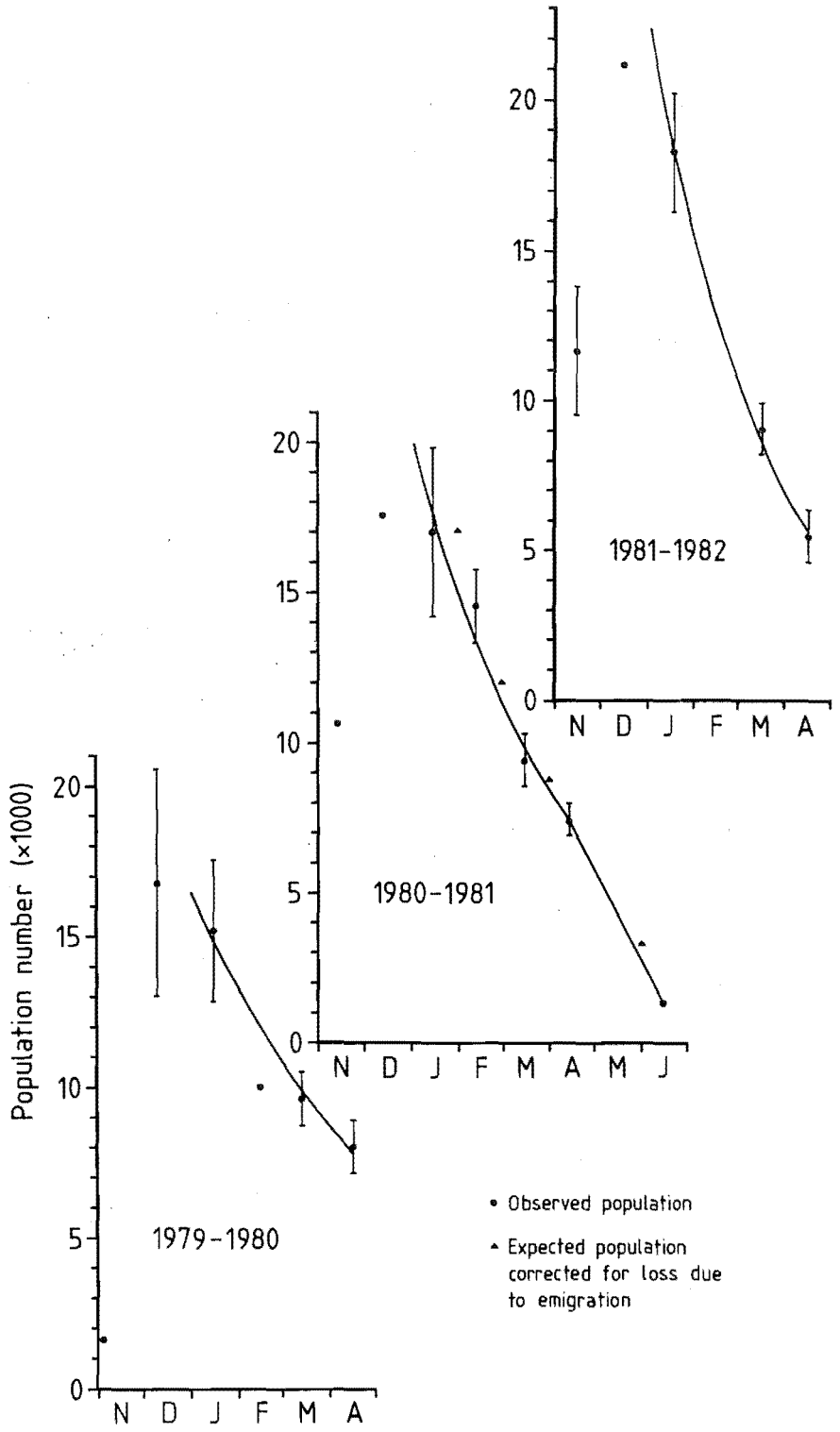


Figure 5.4 Survival curves for 0^+ rainbow trout for three summers (90% confidence limits).

Estimated populations on 1 January 1980, 1981 and 1982 were approximately 16,500, 20,500 and 22,700. Populations of free swimming fry were maximal sometime between the December electrofishing sampling dates and 1 January each year. The population estimates for December 1979 and 1980 are underestimated, since I was unable to obtain declining catches (required for population estimation by the removal method) in the electrofishing runs in some sections, and hence they do not include confidence limits. Recently emerged fry were difficult to catch with the electrofishing apparatus, and therefore population estimates made early in the summer were subject to the most error. In fact, as with densities, variation in the observed maximum populations between years can be explained by sampling error. With this in mind, the maximum population of free swimming fry in all years was probably in the vicinity of 20,000.

Observed populations early in the 1979-1980 summer were lower than those in following years (Fig. 5.4), but this may have resulted partly from less efficient sampling during the first summer. Sampling efficiency was probably lower during that summer because isolation of the sampling sections with stop screens was not as secure as in the following years and the fishing technique improved with practice. In 1979-1980 estimates of total population size were not significantly increased by inclusion of the population between points D and E. Therefore, comparisons between all three survival curves should be valid.

The exponential survival curves assume that mortality was constant over most of the summer. However, the observed loss is a combination of real mortality and emigration. In 1980 I was able to correct observed loss for the emigration component to show real mortality (Fig. 5.4). This procedure reveals that the size of the migration component steadily decreased from January to April and that the mortality rate actually increased (Fig. 5.5). Between April and June observed loss departed substantially from the negative exponential relationship due to

an increase in both emigration and mortality rates (Figs. 5.4 and 5.5). This period coincided with the arrival of adults and onset of spawning in the stream.

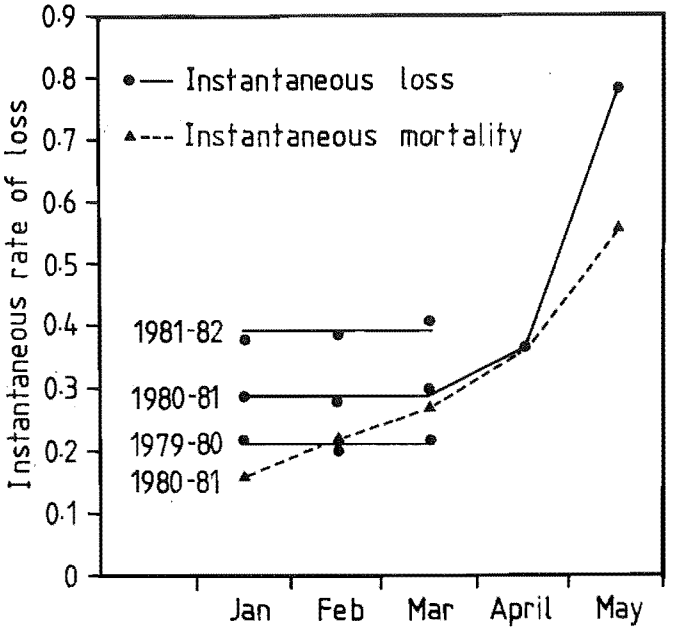


Figure 5.5 Monthly instantaneous loss of 0^+ rainbow trout over three summers.

5.2.6 GROWTH

Arithmetic and geometric mean lengths were calculated for 0^+ brown and rainbow trout respectively, and plotted to produce summer growth curves for each species (Figs. 5.6 and 5.7). Mean length was calculated on a geometric (log) scale for rainbow trout to normalize the positively skewed length distribution as recommended by Sokal and Rohlf (1969). Rainbow trout exhibited little variation in mean length between sampling sections, whereas brown trout exhibited much greater variation

which was caused by small sample sizes (Appendix 2.4). Growth in weight was also determined for each species (Figs. 5.8 and 5.9), monthly mean weights ($\bar{W}$) being calculated from monthly mean lengths ($\bar{L}$) by the length:weight relationships:

$$ln\bar{W} = 3.3447 ln\bar{L} - 12.9201 \qquad (r^2 = 0.9971,\ n = 317) \text{ and}$$

$$ln\bar{W} = 3.1031 ln\bar{L} - 10.9191 \qquad (r^2 = 0.9248,\ n = 794)$$

for brown and rainbow trout respectively. The error in estimating mean lengths and weights was greater for brown trout than for rainbow trout because sample sizes of the former were smaller. Errors in mean weight estimates were greater than those of the mean lengths because of the additional error incurred by regression. The data set for growth in weight of brown trout is incomplete because the errors accumulated in estimating mean weights of the smaller samples of this species were unacceptably large. Growth curves for length and weight of rainbow trout and for weight of brown trout were fitted by the method of successive polynomials (Sokal and Rohlf 1969). However, the final segments of the 1980–1981 and 1981–1982 rainbow trout growth in weight curves were fitted by hand.

The mean size of rainbow trout was always smaller than that of brown trout because of the later emergence of most of the rainbow trout population. At any one time, early emerging rainbow trout of size similar to or larger than the brown trout were more numerous than brown trout, but the influence of such fish on the mean size of the rainbow trout population was negligible, due to the much larger numbers of later emerging fry. Continued recruitment of late emerging fry into the rainbow trout population was responsible for the apparent lack of growth observed in that species during November and the beginning of December (Figs. 5.7

Figure 5.6 Growth in length (95% confidence limits) of 0^+ brown trout in Scotts Creek over three summers (length = arithmetic mean).

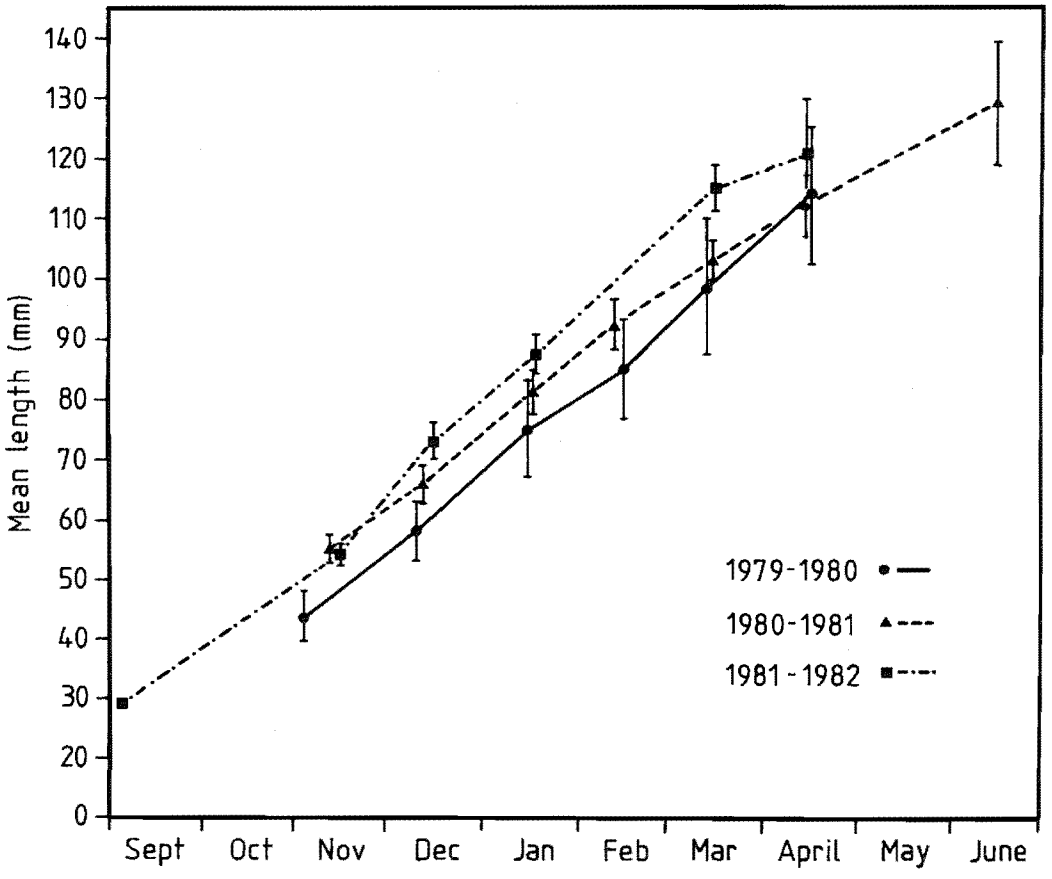


Figure 5.7 Growth in length (95% confidence limits) of 0^+ rainbow trout in Scotts Creek over three summers (length = geometric mean).

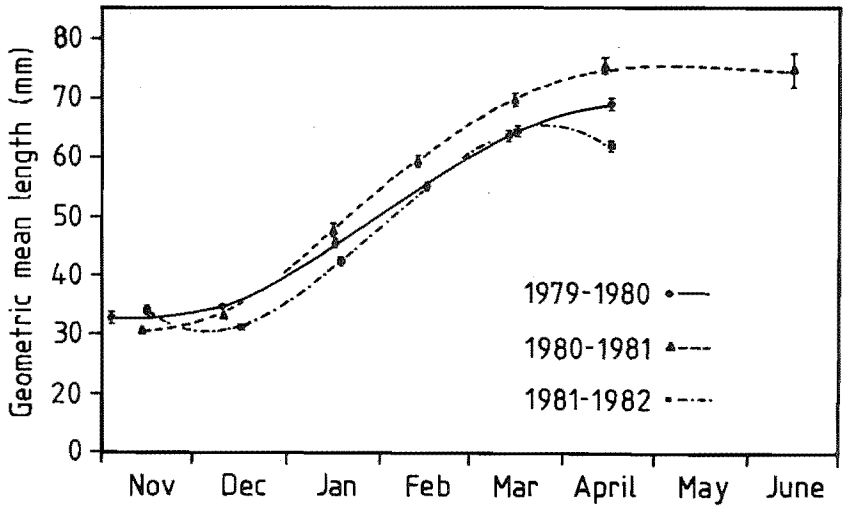


Figure 5.8 Growth in weight of 0^+ brown trout in Scotts Creek over two summers. (95% confidence limits)

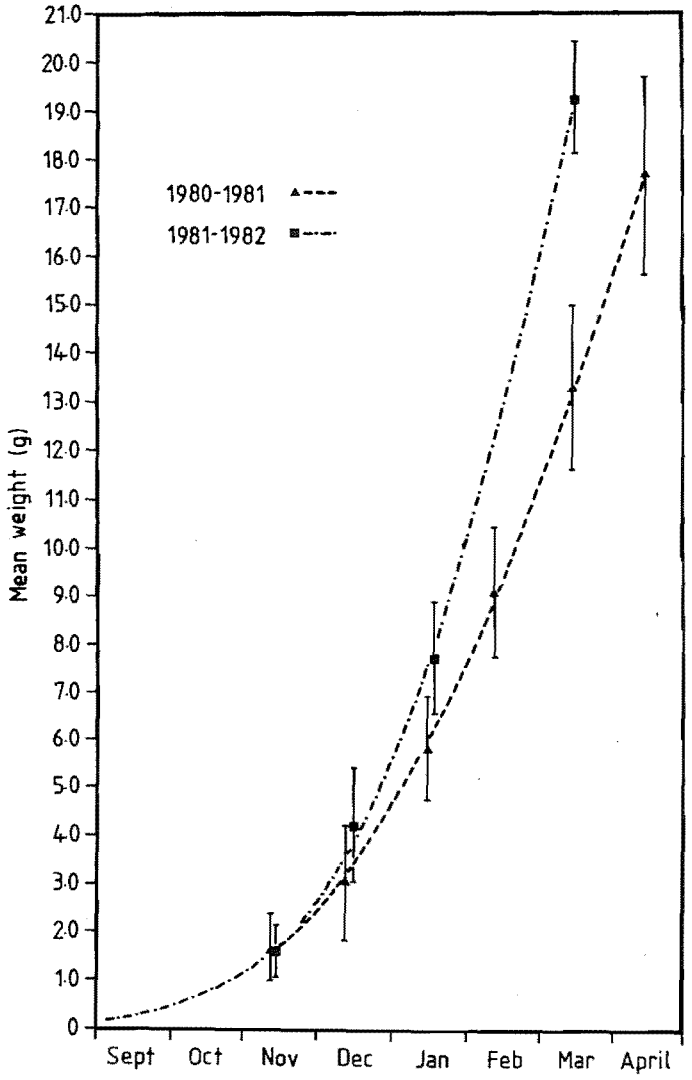
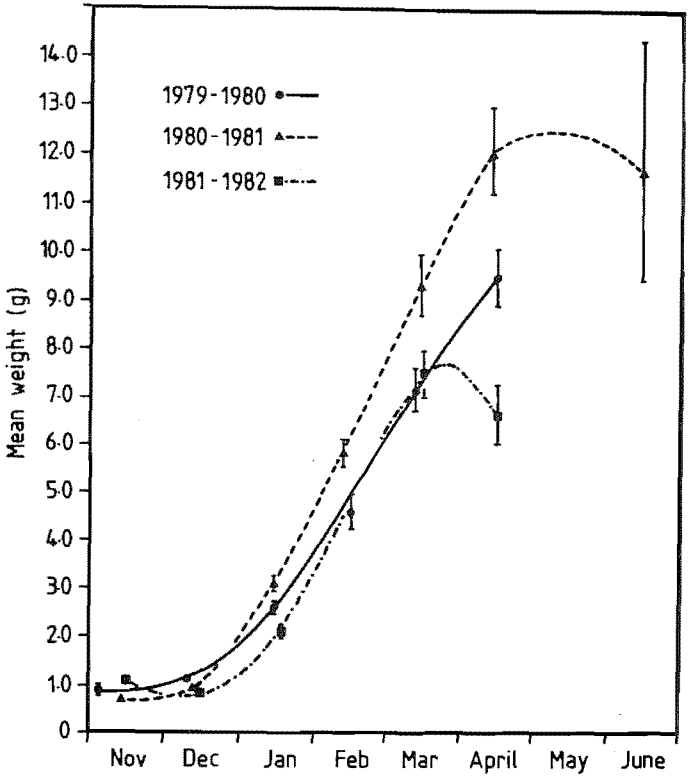


Figure 5.9 Growth in weight of 0^+ rainbow trout in Scotts Creek over three summers. (95% confidence limits)



and 5.9).

Variation in growth between years was not great. Growth rate of both species was highest immediately following emergence and declined over the summer period (Figs. 5.10 and 5.11). Instantaneous growth rates

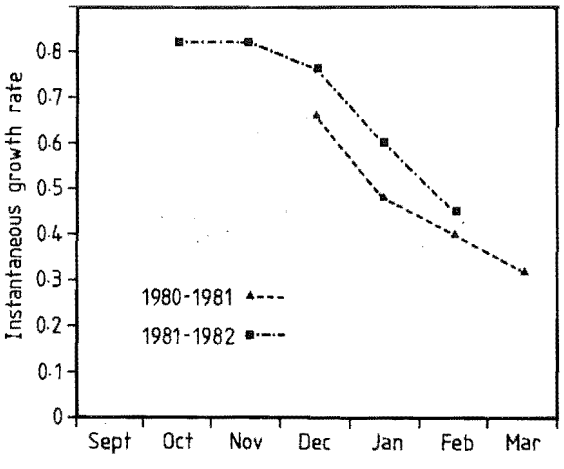


Figure 5.10 Monthly instantaneous growth rate of 0^+ brown trout in Scotts Creek over two summers (calculated from growth in weight curves).

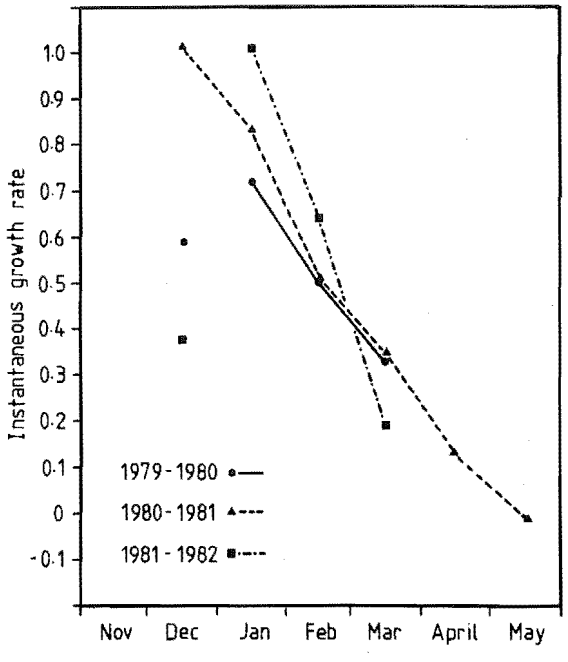


Figure 5.11 Monthly instantaneous growth rate of 0^+ rainbow trout in Scotts Creek over three summers (calculated from growth in weight curves).

of rainbow trout in December 1979 and 1981 were depressed due to recruitment of emergent fry into the populations. Growth rate of rainbow trout declined more rapidly. There appeared to be no relationship between growth and initial densities of rainbow trout but, as mentioned previously, differences in initial density estimates may simply have been due to sampling error. Highest growth rates for both species occurred in 1981–1982 (Figs. 5.10 and 5.11). However, mean monthly sizes of rainbow trout were greatest in the summer of 1980–1981 (Fig. 5.9). The smaller

size attained by rainbow trout in 1981-1982 than in 1980-1981, in spite of a higher growth rate, was due to delayed peak emergence in 1981-1982. This was indicated by high densities of emergent fry and consequently apparently depressed growth of rainbow trout occurring further into December of that summer. The 1980-1981 and 1981-1982 rainbow trout growth curves and their associated instantaneous growth rates (Figs. 5.9 and 5.11), indicate that growth declined and became negative from April to June and from March to April respectively in the two seasons. However, this decline in observed growth appeared to be partly due to size selective emigration. Observed growth is effected by size selective mortality and migration. For the 1980-1981 sampling period I was able to investigate the effect migration of underyearlings had on the observed growth rates of the two species. Comparison of monthly mean lengths and length distributions of residents and migrants revealed that in rainbow trout, but not in brown trout, significant size selective emigration occurred and could account for changes in observed growth (Figs. 5.12 and 5.13). The apparent reduction in growth from April to June can be explained by larger fish tending to emigrate; migrants were significantly larger than residents in June (Fig. 5.13). Migrants were also significantly larger than residents in March. However, in November and December migrants were significantly smaller than residents, due to emigration of recently emergent fry during this period. There was no significant difference in mean lengths between migrant and resident underyearling brown trout during the 1980-1981 sampling period, but sample sizes, particularly of residents, were small.

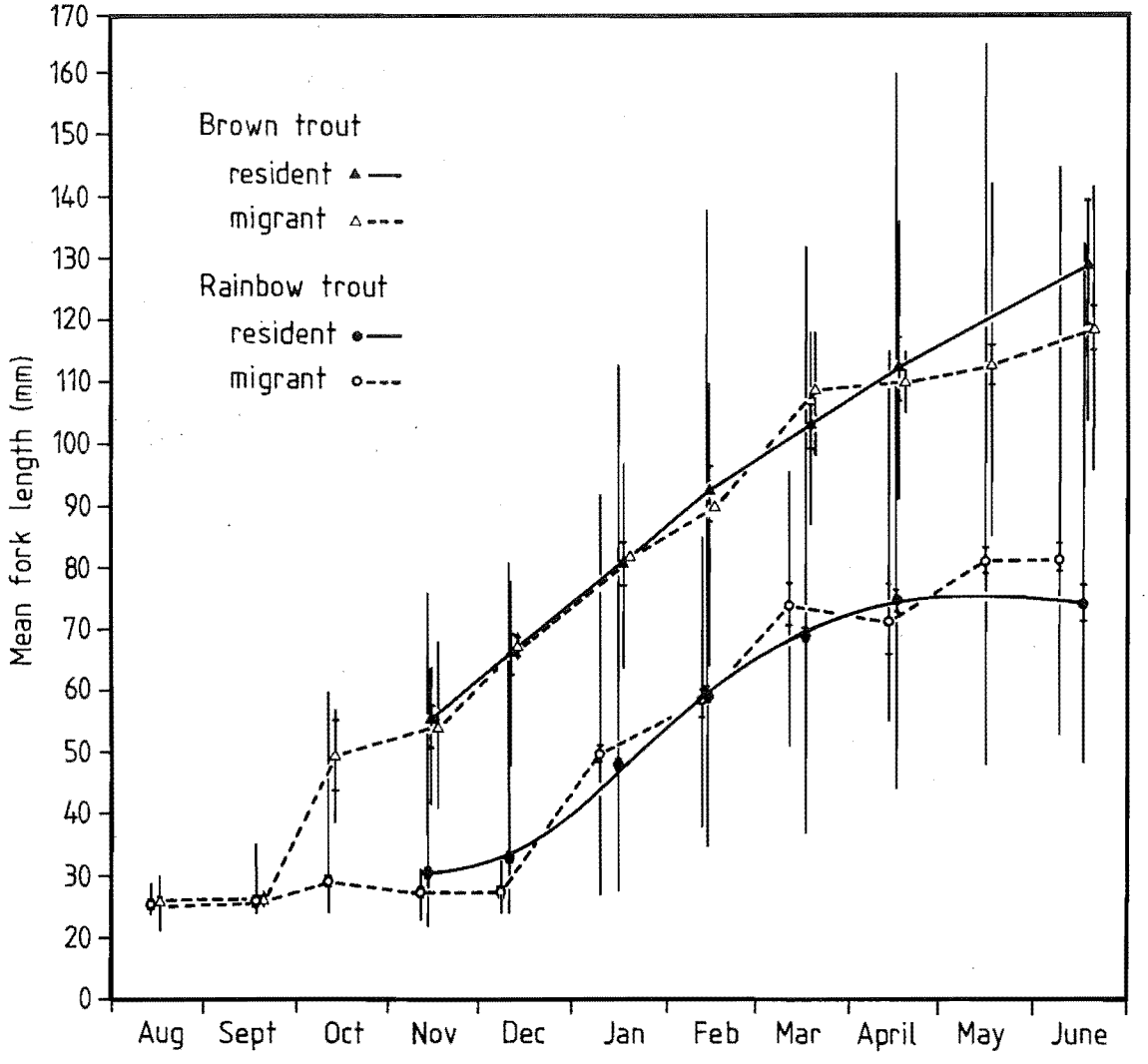


Figure 5.12 Comparison between monthly mean lengths (95% confidence limits and range) of resident and migrant underyearlings for brown and rainbow trout over the 1980–1981 summer.

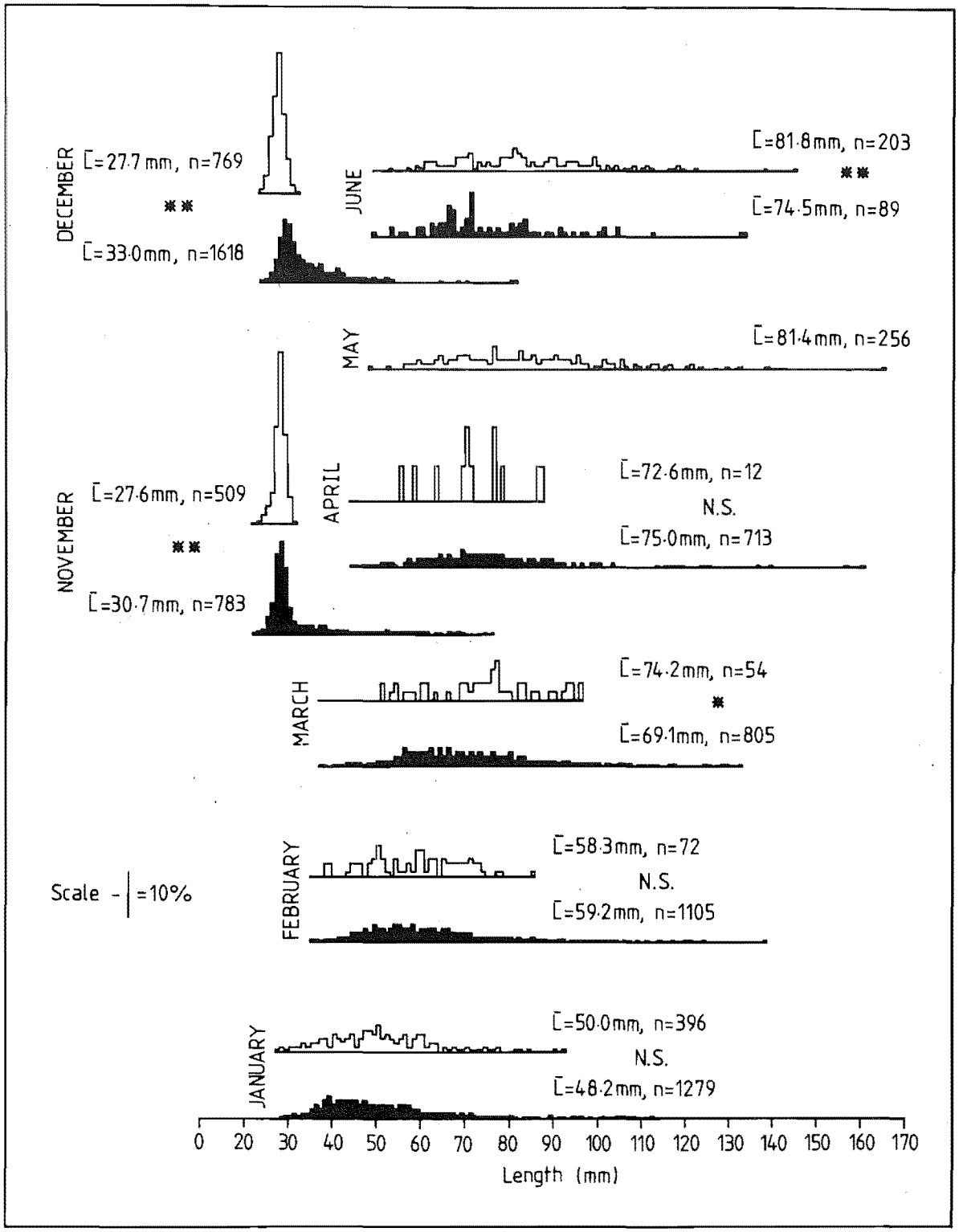


Figure 5.13 Comparison between resident and migrant 0^+ rainbow trout monthly length percent frequency distributions over the 1980–1981 summer (* and ** represent 0.05% and 0.01% significance levels for U test between the two distributions).

5.2.7 BIOMASS

Monthly estimates of biomass (density x mean weight ($\bar{W}$)) were calculated for 0^+ rainbow trout between points A and B in Scotts Creek (see Fig. 2.2) for the three summer sampling periods (Table 5.5), using combined monthly mean densities from Sections 1 and 2 and monthly mean weights from Figure 5.9. Biomass of 0^+ rainbow trout approximates total biomass of 0^+ salmonids in Scotts Creek. Biomass estimates were confined to the population between points A and B because this stretch of stream provided the best comparative data between years: it was the major juvenile rearing area, it was not subject to temporary population fluctuations as were the peripheral areas further upstream, and its representative sampling sections (Sections 1 and 2) were the most often sampled over the three summers.

Monthly estimates of biomass during the summer growing period after the end of emergence (i.e. January to April) were greatest in 1981. Very similar monthly biomass was recorded for the 1979-1980 and 1981-1982 summers during the period December to March. November biomass was variable between years due to variation in times of sampling and peak emergence. Large reductions in biomass occurred during the periods April to June 1981 and March to April 1982 and apparently were caused largely by emigration, and possibly mortality, of the larger underyearlings. Variations in biomass between years appeared to be related more to variations in growth than in density.

Table 5.5 Monthly estimates of biomass of 0^+ rainbow trout between points A and B in Scotts Creek over three summers.

	1979-1980			1980-1981			1981-1982		
	Mean density (m^{-2})	$\bar{W}$ (gm)	B.($gm.m^{-2}$)	Mean density (m^{-2})	$\bar{W}$ (gm)	B ($gm.m^{-2}$)	Mean density (m^{-2})	$\bar{W}$ (gm)	B ($gm.m^{-2}$)
November	0.5	0.9±0.1	0.45	3.2	0.7±0.1	2.2	3.7±0.8	1.1±0.1	4.1±1.3
December	4.9±1.4	1.1±0.1	5.4±2.0	5.4	0.9±0.1	4.9	6.3±0.6	0.8±0.1	5.0±1.1
January	4.5±0.8	2.6±0.1	11.7±2.5	5.2±0.8	3.1±0.2	16.2±3.5	5.3±0.7	2.1±0.1	11.1±2.0
February	2.7±0.6	4.5±0.3	12.2±5.6	4.4±0.4	5.8±0.3	25.5±3.6			
March	2.6±0.3	7.1±0.5	18.5±3.4	2.8±0.3	9.3±0.6	26.0±4.5	2.6±0.3	7.4±0.5	19.2±3.5
April	2.3±0.3	9.4±0.6	21.6±4.2	2.1±0.2	12.0±0.9	25.2±4.3	1.5±4.3	6.6±0.6	9.9±2.9
June				0.4	11.6±2.5	4.6			

5.2.8 PREDATION ON FRY

5.2.8.1 METHODS

In the latter half of the 1980 spawning season, I investigated the possibility that numbers of early emerging fry might be reduced by predation by adult trout present in the spawning stream. From 18 July 1980 to 6 October 1980 I sampled the gut contents of 88 spent rainbow trout (52 females and 36 males) and two spent brown trout (1 male and 1 female), with a gut evacuation pump described by Griffiths (1976).

5.2.8.2 RESULTS

None of the fish examined contained fry in their stomachs. The most common food item was trout eggs (Table 5.6). These occurred in 20% of fish examined and accounted for about 95% of total gut contents . One fish had consumed 342 eggs.

On the other hand fry were eaten by yearling rainbow trout. On numerous occasions over the emergence period, particularly during peak emergence, yearlings captured in the fry trap had gorged themselves on emergent fry. However, this predation was artificially facilitated since the fry had been confined with the yearlings in the fry trap. A sample of five resident yearlings taken from the stream early one morning during peak rainbow trout fry emergence in 1981 (i.e. at the beginning of December) revealed that these fish did indeed prey on emergent fry. All five yearlings contained fry; the numbers eaten ranged from 5 to 30 with a mean of about 20 per fish.

Table 5.6 Gut contents of 90 spent adults taken from Scotts Creek between 18 July and 6 October 1980. (l = larvae)

Item	Occurrence No.	Occurrence %	Number No.	Number %
MOLLUSCA				
Gastropoda				
Hydrobiidae				
Potamopyrgus antipodarum	3	3	12	2.4
ANNELIDA				
Oligochaeta				
Lumbricidae	1	1	1	0.2
ARTHROPODA				
Insecta				
Ephemeroptera				
Leptophlebiidae				
Deleatidium sp. (l)	6	0.7	6	1.2
Hemiptera				
Corixidae				
Sigara arguta	1	1	1	0.2
Trichoptera				
Hydrobiosidae (l)	2	2	2	0.4
unidentified (l)	3	3	3	0.6
Trout eggs	18	20	469	94.9

5.2.9 GUT CONTENTS OF UNDERYEARLING BROWN AND RAINBOW TROUT

5.2.9.1 METHODS

A comparative investigation into the diets of 0^+ brown and rainbow trout was undertaken over the summer of 1979-1980. Fish were collected by electrofishing at monthly intervals in conjunction with the regular sampling programme, but were taken from areas outside the regular sampling sections. Comparative information on diets was limited by the very small sample sizes of brown trout obtainable. Only 21 brown trout were collected over the entire summer. A sample of 27 rainbow trout was used for comparison with the browns. Selection of these fish was made on the basis of similar size and dates of capture to those of the brown trout. The fish were preserved in 10% formalin and the gut cavities of larger fish were injected with formalin. Later, guts were dissected from the fish and individual food items in the stomachs were identified to species level where possible and counted. Gut contents were analysed by the numerical and occurrence methods (Hynes 1950).

5.2.9.2 RESULTS

Brown and rainbow underyearlings ate similar invertebrate food items but rainbow trout utilized a wider variety than brown trout (Table 5.7). Rainbow trout had a higher mean number of food items in their stomachs than brown trout i.e., 19.3 per fish compared with 6.9 per fish. The wide variety of food items eaten would have been due partly to the extended period over which the samples were taken, since occurrence and abundance of many of the invertebrates would have varied with time of the season. In this study, occurrence of food items is more informative than

Table 5.7 Gut contents of 0^+ brown and rainbow trout taken from Scotts Creek in the summer of 1979-80. (l = larvae, p = pupae, a = adults)

	Occurrence				Number			
	Brown		Rainbow		Brown		Rainbow	
	No.	%	No.	%	No.	%	No.	%
MOLLUSCA								
Gastropoda								
Planorbidae								
Gyraulus sp.			1	3.7			3	0.6
Physidae								
Physa acuta	2	10.5	2	7.4	15	13.9	10	1.9
ANNELIDA								
Oligochaeta								
Lumbricidae			2	7.4			2	0.4
Tubificidae			1	3.7				
ARTHROPODA								
Crustacea								
Cladocera								
Daphniidae								
Ceriodaphnia dubia			1	3.7			1	0.2
Simocephalus vetulus	1	5.3			1	0.9		
Chelicerata								
Acarina								
Hydracarina			1	3.7			1	0.2
Insecta								
Collembola			3	11.1			44	8.6
Ephemeroptera								
Leptophlebiidae								
Deleatidium sp. (l)	6	31.6	15	55.5	10	9.3	49	9.5
Odonata								
Coenagrionidae								
Xanthocnemis zealandica (l)			1	3.7			1	0.2
Hemiptera								
Corixidae								
Sigara arguta	4	21.1	5	18.5	7	6.5	12	2.3
Thysanoptera								
Thripidae			1	3.7			1	0.2
Coleoptera								
Helodidae (l)	3	15.8			12	11.1		
unidentified (a)			1	3.7			3	0.6
Diptera								
Tipulidae (l)			5	18.5			6	1.2
Dixidae (p)			3	11.1			22	4.3
Chironomidae (l)	4	21.1	21	77.8	8	7.4	202	39.3

Cont'd over/....

	Occurrence				Number			
	Brown		Rainbow		Brown		Rainbow	
	No.	%	No.	%	No.	%	No.	%
Chironomidae (p)	1	5.3	7	25.9	27	25.0	21	4.1
Ceratopogonidae (l)	1	5.3	4	14.8	1	0.9	7	1.4
Simuliidae (l)			2	7.4			3	0.6
Sciaridae (a)			1	3.7			6	1.2
Ephydridae (a)			1	3.7			1	0.2
unidentified (a)	3	15.8	2	7.4	3	2.8	3	0.6
Trichoptera								
Hydrobiosidae								
Hydrobiosis umbripennis (l)			1	3.7			1	0.2
unidentified (l)	1	5.3	2	7.4	1	0.9	2	0.4
Conoesucidae								
Pycnocentria spp. (l)			1	3.7			3	0.6
Pycnocentrodes sp. (l)			3	11.1			9	1.8
Hydroptilidae								
Oxyethira albiceps (l)	3	15.8	10	37.0	7	6.5	85	16.5
Oeconesidae								
Oeconesus sp. (l)			2	7.4			2	0.4
Leptoceridae								
Hudsonema amabilis (l)	2	10.5	2	7.4	16	14.8	6	1.2
unidentified (l)	1	5.3	2	7.4	1	0.9	2	0.4
unidentified (a)			2	7.4			2	0.4
Lepidoptera								
unidentified (l)			1	3.7			1	0.2
Hymenoptera								
unidentified (a)			1	3.7			1	0.2
FISH (unidentified)	1	5.3			2	1.9		

number of each item eaten, since with small samples taken over a long time period numerical analysis is too sensitive to temporal and spatial variations in abundance of individual food items and can produce misleading results.

The most frequently occurring items in the diet of both brown and rainbow underyearlings were nymphs of the mayfly genus Deleatidium and chironomid larvae. Food of terrestrial origin

appeared more numerous in the diet of rainbow trout (25.9%), than brown trout (15.8%), but the difference between the species was not significant when tested with Chi-square.

5.3 DISCUSSION

5.3.1 EMERGENCE AND OUTMIGRATION OF JUVENILES

The 0^+ salmonid populations in Scotts Creek were dominated by late emerging rainbow trout. In 1980 total fry output from the redds was at least 439 brown and 203,474 rainbow trout, with the larger total for rainbow trout composed mainly of late emerging fry. Although rainbow trout were numerically dominant over brown trout the stream was used more by the latter as a juvenile rearing environment, since approximately 73% of brown trout and only 10% of rainbow trout remained in the stream after emergence. Thus underyearling output from the stream into the lake is dependent in brown trout on late migrants (approximately 61% had spent some time rearing in the stream), and in rainbow trout, is heavily dependent on early migrants (approximately 96% were recently emerged fry). The difference between the species resulted from a greater degree of downstream dispersal by emergent rainbow fry, producing a large nocturnal outmigration of fry into the lake. Similar nocturnal downstream migration of emergent fry has been reported for rainbow trout by Hartman (1958), Northcote (1962), Everest (1971), Stauffer (1972), Alexander and MacCrimmon (1974) and Erman and Leidy (1975); for brown trout by Elliott (1966), Cuinat and Heland (1979), Heland (1980a,b) and Ottaway and Clarke (1981); and for other salmonid species by MacKinnon and Brett (1955), Neave (1955), Hoar (1956,1958), Hartman, Strickland and Hoopes (1962), Au (1971), Reimers (1973) and Unwin (1984). However, downstream migration

upon emergence, at least in rainbow trout, is not obligatory. Northcote (1962) reported that recently emerged rainbow trout in an outlet stream of Loon Lake, British Columbia maintained their position at night and moved upstream during the day, whereas fry in inlet streams exhibited nocturnal downstream dispersal and little upstream movement. Nocturnal downstream movement occurred when water temperatures were below 13°C (characteristic of Loon Lake inlet streams). Water temperatures in Scotts Creek during downstream migration of fry were consistently below 13°C. Recent work by Kelso, Northcote and Wehrhahn (1981) suggested that lakeward migration of young rainbow trout in British Columbia was determined by both environmental and genetic factors.

Salmonid fry and juvenile migrations have been suggested as a population regulating mechanism by several writers (e.g, Kalleberg 1958, Onodera 1962, Hunt 1965, Johnson 1965 and LeCren 1965). This hypothesis is supported by evidence presented by LeCren (1961), Chapman (1962,1966), Mason and Chapman (1965) and Mason (1969) for aggression-induced downstream migration of fry. However, the commonly observed downstream movement of fry upon emergence appears to be largely a passive dispersal, dependent on current speed and turbulence and on characteristic behaviour patterns of the emergent fry (Au 1971). Bams (1969) showed that sockeye salmon fry increased their activity and moved to the gravel surface during maximum water temperatures in the afternoon. Under the normal light:dark cycle, actual emergence of these fish from the gravel was inhibited until light levels decreased at dusk. Reimers (1973) found that, in observation troughs, under the normal light:dark cycle most chinook salmon fry emerged in darkness, mainly in the evening period, and immediately "disappeared" downstream. A characteristic feature of nocturnal downstream dispersal of emergent fry is the inhibiting effect of moonlight, which presumably also inhibits emergence. Reimers considered that, since most emergence and downstream movement probably

occurred on the same night, there would be little opportunity for interaction among fry. Further evidence against socially induced nocturnal downstream migration of emergent fry comes from observations made in the present study, and by Au (1971), of fry dispersing downstream at various population densities and even when no resident fry were present. A number of authors have suggested that the behaviour associated with obtaining air for the swim bladder from the surface upon emergence initially the direct cause of displacement (Kalleberg 1958, Bams 1969, and Au 1971). Air gulping is characterized by darting, struggling motions toward the surface, obviously making fry vulnerable to downstream displacement by the current. Thomas, Banks and Greenland (1969) postulated that the observed reduced swimming ability of chinook salmon alevins shortly after yolk absorption was a cause of fry displacement, and Reimers (1973) thought that this was the key factor facilitating immediate downstream dispersal of emergent fry of this species. Hoar (1958) postulated that reactions (both visual and tactile responses) which orient fish both in the current and in their hiding places among stones during the day will be reduced at night, and that fish losing direct contact with the bottom will swim or drift with the current. Behaviour which reduces nocturnal activity and maintains contact with the substrate promotes maintenance of position. Older resident underyearlings are usually quiescent at night and rest on or over the bottom in areas sheltered from fast currents. This behaviour was observed, for example, in brown and rainbow trout in the present study, in rainbow trout by Northcote (1962) and in coho salmon by Hoar (1951) and Smirnov (1960).

Expanding on the ideas of Hoar (1958), both Au (1971) and Reimers (1973) proposed a mechanism for nocturnal downstream dispersal of emergent fry, which appears to be compatible with the pattern of emergent fry migration and stream colonization by fry observed in Scotts Creek. They postulated that dispersal is initiated by nocturnal emergence,

involves lack of visual orientation by fry at low light intensities, and is augmented by the initial disequilibria of the emerged fry and by water velocity and turbulence. Dispersal ceases as fry develop nocturnal resting behaviour, i.e. the seeking of sheltered spots near the bottom of pools and stream margins. Such behaviour is pictured as developing rather gradually over several days as a process of fry maturation. Au (1971) states that "if the development of this new form of behaviour (nocturnal resting behaviour) is delayed due to stress or the inability of the fry to obtain sufficient food or space requisites, dispersal continues. If this is true, then it can be seen how the particular developmental condition of fry upon emergence, the inherent suitability of stream sections to provide the requirements of food and space, and competition with other fry for the latter all interact to control "dispersiveness"". There is therefore considerable variation amongst dispersing fry in their readiness to settle. Thus stream colonization is accomplished over a prolonged period by a continuous recruitment from a series of dispersing waves of fry. As resident fish grow they move into faster deeper water (Lister and Genoe 1970, Everest and Chapman 1972, Kennedy and Strange 1982) thereby vacating habitat which becomes available for further colonization.

The much greater proportion of rainbow trout than brown trout leaving the stream as emergent fry was probably a reflection of differences in "dispersiveness", caused by differences in the behaviour patterns of emergent fry of the two species. The high nocturnal activity of emergent rainbow fry in the water column and at the surface, compared with the low activity and greater substrate association of emergent brown fry, would make rainbows more susceptible to downstream displacement.

Emergent rainbow fry in Scotts Creek had a high dispersal capability; some marked fry were observed to travel at least 1km in one night. In comparison, Au (1971) recorded maximum distances travelled by

coho salmon fry at between 230m and 320m per night. Northcote (1962) reported that one third of recently emerged rainbow fry released 305m above a fry trap on an inlet stream of Loon Lake were recovered on the first night, and 50% had been recovered after the second night following release. Since the spawning ground in Scotts Creek extends only 1.5km upstream from the lake, such high "dispersiveness" results in the majority of rainbow trout emigrating to the lake possibly on the night of, or on nights soon after, emergence. The much lower dispersal exhibited by emergent brown trout in the present study, in which only 27% migrated to the lake as emergent fry, is very similar to the dispersal observed for brown fry in the Lissuraga Brook by Cuinat and Heland (1979), who recorded 28% of planted recently emerged fry migrating at night from a study section of stream.

Nocturnal dispersal of fry probably minimizes predation and minimizes energy expenditure necessary for adjusting population abundance (through social interactions) in streams in relation to food and space. Translocation, by such dispersal, to a lentic environment enables the majority of rainbow trout emerging in Scotts Creek to completely avoid the pressures of population regulation imposed by spatial restrictions of a lotic environment. Synchronization of emergence and subsequent dispersal should further serve to minimize predation through predator saturation. Synchronization of dispersal occurs daily, with most fry dispersing soon after the onset of darkness, and it also occurs on a monthly basis when periods of high lunar illumination inhibit, and thus delay, dispersal (and probably emergence) until the onset of periods of low nocturnal illumination.

Once fry establish stream residence behaviour and begin expanding their territories, density dependent competition between fry, mediated through agonistic behaviour, will become important in regulating populations by affecting movement, mortality and growth. However,

socially related population regulation will occur only if densities are high enough for serious competition to occur. In Scotts Creek, high densities of fry did not occur until the period of peak emergence of late emerging rainbow fry in late November and December. Actual maximum densities of fry at that time would have been higher than the 7.67 fry.m^{-2} calculated on the basis of total area available, due to the preferential use of specific habitats by the large numbers of similar sized late emerging fry. Much of the outmigration of post-emergent rainbow fry (i.e., fry that had spent some time living in the stream) during October 1980 to March 1981, and particularly in late December and January, possibly resulted from increasing intraspecific competition for space between these late emerging individuals.

Downstream migration of post-emergent brown and rainbow trout also took place mainly at night. Chapman (1962) and Au (1971) reported that with post-emergent 0^{+} coho salmon a much greater proportion of fry movement occurred during the day, which was considered to reflect the increasing importance of diurnal agonistic activity. However, Stauffer (1972) observed that most downstream migration of post-emergent rainbow juveniles in a Lake Michigan tributary occurred at night. Reimers (1973) found that subordinate chinook salmon fry that were nipped or threatened all day did not move downstream until dusk. Lack of diurnal migration might be related to the physical characteristics of the stream, for example predation may select against diurnal migration in streams such as Scotts Creek which are small, clear and shallow providing little overhead cover for protection from avian or terrestrial predators. It was also likely that in the present study the confined nature of, and lack of overhead cover on, the lead-in chute of the fry trap caused potential diurnal migrants to avoid entering the trap during the day.

5.3.2 MORTALITY

Socially mediated intraspecific competition among rainbow trout may actually have been more important in regulating mortality than movement over the summer growing season, since from January to April 1981 the migration rate declined whereas the mortality rate increased. Egglishaw and Shackley (1980) suggested that most of the loss they observed in Atlantic salmon fry over the summer was due to mortality rather than movement. Au (1971) reported that 0^+ coho salmon also exhibited little downstream movement but considerable mortality over the summer growing season. He concluded that "the major importance of agonistic territorial behaviour must lie in the regulating of mortality and growth processes".

Published studies on very young fish indicate that their survival may conform well to the negative exponential model (Chapman 1978). In Scotts Creek, observed loss in numbers of 0^+ rainbow trout over the summer growing period for three consecutive years conformed to negative exponential relationships. A number of writers have shown that salmonid fry which are resident in streams experience heavy mortality during the first few months of life (e.g., Alm 1950, Allen 1951, Hunt 1965, Latta 1962, LeCren 1965, Mortensen 1977c), often considerably more than 90% for the first six months or so (Allen 1962). Evidence from such studies suggests that this mortality is density dependent and operates through competition between fry for space. Over the four months after emergence for which reliable population estimates were made in Scotts Creek, from January to April, observed loss of 0^+ rainbow trout was approximately 30, 43 and 53 percent in 1980, 1981 and 1982 respectively. It is not possible to estimate accurately the loss from emergence to April because of the prolonged emergence period. However, a crude estimate was be calculated for the 1980-1981 season for which I had the

most complete data set. Total output of fry from redds that season was more than 203,474, most of which emerged during November and December. By April only 7,500 were left in the stream and by June only 1,500, giving an observed loss for the first six months and for the first eight months of approximately 96% and 99% respectively. In comparable studies on mortality of juvenile trout in other New Zealand streams, Allen (1951) estimated that 44% of brown trout died before beginning to feed and only 2% of young were alive after three months in the Horokiwi Stream. Hopkins (1970) estimated that the mortality of brown fry in the Hinau and Hinaki streams was approximately 90% over the first four months of life. In an inlet spawning and nursery tributary of Lake Eucumbene, Australia, mortality of 0^+ brown trout was approximately 96% and 98% over the first four and six months respectively (Tilzey 1972). Much of the observed summer loss recorded in the present study, particularly soon after emergence, could be attributed to emigration from the study area to the lake.

When the emigration component of observed loss in 1981 was accounted for it was found that, rather than being constant as the observed loss suggested, true mortality within the study area actually increased over the summer. Obviously a proportion of the outmigrants would also have died, but outside the study area. Most published studies reporting mortality have simply recorded observed loss, and incidentally acknowledged the potential effects of movements on loss. The above results suggest that caution should be exercised when drawing inferences about mortality from observed loss, since observed loss can be meaningless as an indicator of mortality. Mortality could result from predation, starvation, disease or injury acting either alone or in combination. Intraspecific predation by yearling rainbow trout on fry was observed as was interspecific predation between underyearlings, although the latter is likely to be insignificant. Cannibalism by parents has been

suggested as an effective population regulator (McFadden 1968) but appeared to be negligible within Scotts Creek, at least during the fry stage when potentially it would be most effective. Large longfinned eels (Anguilla dieffenbachii) are present in Lake Alexandrina and Scotts Creek and are known to eat trout; for example, Cairns (1942) found that trout occurred more commonly than any other type of food in longfinned eels more than 0.76m in length in some New Zealand waters. With regard to the present study area, Hobbs (1948) reported the occurrence of eight eels weighing a total of 24.5kg in a small section of Scotts Creek, and of these five contained trout fingerlings. Hobbs suggested that control of these predators in such trout nursery areas would be beneficial to a fishery. Recruitment of eels into Lake Alexandrina through upstream migration of elvers ceased in 1965 when the second of a series of hydro dams and water control structures was constructed on the Waitaki River downstream from Lake Alexandrina. This development, together with a limited amount of commercial fishing for eels in Lake Alexandrina, has presumably led to a decline in the eel population which will continue in the future. Numbers of eels in Scotts Creek now appear to be low and this predator now probably contributes little to the mortality of trout either in the stream or in the lake. Over my entire sampling period, only five eels were encountered in Scotts Creek, one of which contained two fingerlings. Terrestrial predators which frequent the stream include white faced herons (Ardea novaehollandiae), white herons (Egretta alba), black shags (Phalacrocorax carbo), black-fronted terns (Chilidonias albostriatus), kingfishers (Halcyon sancta) and Australian brown bitterns (Botaurus poiciloptilus), of which the white faced heron would be the most important. Apparent starvation (LeCren 1962,1965) and nutritional insufficiency (Gardiner and Geddes 1980) probably account for a large proportion of deaths of recently emerged fry. Death from

physical exhaustion due to intraspecific competition was reported by Miller (1958), and Glova (1978) described indirect mortality caused by Saprolegnia sp. infections of injuries from aggressive nipping.

Living space for the larger juveniles (i.e., larger than about 100mm) may have become limiting over the late summer to early winter of 1981. Evidence for space limitation was seen in the larger numbers of both species migrating in the autumn and early winter, and in the greater mean length of migrant than resident 0^+ rainbow trout in March and June. There appeared to be little habitat in the form of deep fast water and overhanging cover in Scotts Creek for these larger juveniles. The low numbers of 1^+ and 2^+ fish also suggest this habitat shortage. Increased outmigration of underyearlings in the autumn and early winter may also have been related to the arrival of adults returning to spawn in the stream. Outmigration of juveniles coinciding with upstream migration of spawning adults has been reported by Stuart (1957) for brown trout and Unwin (1984) for chinook salmon. In Scotts Creek, adults congregated in the deep fast flowing areas and under overhanging banks, and hence probably displaced the larger underyearlings which also utilized these habitats. Adults may also have been responsible for the increased loss of underyearlings between April and June 1981. Occupation of the same habitat as adults would expose the larger underyearlings to a greater risk of predation from adults. The habit of large underyearlings of frequenting occupied redd sites to eat eggs of spawners would also increase their risk of mortality from attack by males guarding the sites. Such attacks were observed and crushed fingerlings were encountered when adults began spawning in 1981.

5.3.2 GROWTH

Growth rates of trout in New Zealand appear to be high in comparison with waters elsewhere, particularly those in Europe. Weatherly and Lake (1967) considered growth rate of trout in New Zealand and Tasmania to be similar, and higher than in Great Britain. They concluded that general regional differences between trout growth rates can be accounted for in terms of climatic differences. Growth rate of trout in Scotts Creek was approximately five times greater than that recorded by Egglishaw and Shackley (1977) for underyearling brown trout and Atlantic salmon in a small Scottish stream, and more than twice as fast as growth of rainbow trout observed by Hartman (1958) in an inlet stream in the Finger Lakes region New York, U.S.A.. Within New Zealand, growth rate of trout in Scotts Creek was slightly lower than that recorded for underyearling brown trout in the Horokiwi Stream by Allen (1951) and in the Hinau and Hinaki streams by Hopkins (1970).

Two major extrinsic factors influence growth rate, temperature and competition for food (Weatherly and Rogers 1978). Backiel and LeCren (1978) postulated that density effects on fish populations operate mainly through mortality early in life, and through growth later in life. In the present study, initial densities of fry (after completion of emergence) were relatively similar between years, which is to be expected if (as hypothesized) egg capacity of the spawning bed is exceeded each year by late spawners. Densities between years remained similar and rate of loss was constant over much of the summer growing period (at least until March) whereas growth was more variable. This perhaps suggests less dependence by growth than by mortality on density. Variation in biomass between years during this period was thus influenced more by growth than by density. Growth rates of underyearlings declined over the summer possibly reflecting increased demands on food and space as the fish

became larger, but more probably growth was responding to the decline in water temperature and thus conforming to the seasonal cycle commonly observed in fish populations (Ricker 1979). The high instantaneous growth rates following emergence were maintained for a longer period by brown trout than by rainbow trout, probably because of the longer optimal growing conditions (with earlier emergence) experienced by that species compared with the bulk of the rainbow trout population. Thus, the larger mean size attained by brown trout was due to the shorter growing season experienced by the bulk of the rainbow trout population. For rainbow trout, length of this growing season, and hence size attained, was dependent on timing of peak emergence. Rainbow trout do have a similar growth potential to brown trout as was shown by some individuals, presumably early emergers, which achieved lengths similar to those of brown trout.

Observed growth can be affected by size selective migration and mortality. In the present study, the rapid decline in observed growth, and associated occurrence of negative growth rate, of rainbow trout, in the autumn and early winter of 1981 can be largely attributed to selective migration and possibly mortality of the larger juveniles, possibly induced by entry of adults into the stream. A similar decline in growth of rainbow trout between March and April 1982 was also probably due largely to selective migration, and possibly mortality of large residents; implied by a corresponding large drop in density. However, such size selective migration (and mortality) cannot have been induced that year by spawners since it occurred prior to their arrival in the stream. A dry summer, and improved drainage of swampland over a large area of the catchment, contributed to lower late summer flows that season. This could have brought about a critical shortage of habitat for larger underyearlings, which would increase their mortality and emigration rates.

Comparison of monthly estimates of biomass between years gave a clearer understanding of differences in carrying capacity between years. Biomass was greater over much of the summer of 1980-1981 than in the preceding and following summers. Greater biomass that summer resulted from greater growth rather than from higher densities, and reflects more favourable growth conditions in 1981.

In summary, the juvenile salmonid populations in Scotts Creek were dominated by late emerging 0^+ rainbow trout, despite a much greater tendency shown by brown trout to remain in the stream following emergence. This situation arose because of the much greater escapement of late than early emerging fry from the redds due to effects of redd superimposition during the spawning season. In this respect intraspecific competition for spawning space profoundly influenced the pattern of emergence and subsequent population structure of underyearling rainbow trout in Scotts Creek. Living space for underyearlings did not appear to be in short supply until late in the emergence period when the bulk of the rainbow trout population had emerged. Space, particularly for larger underyearlings, may have become limiting during late summer when mortality increased. Earlier emergence by brown trout gave s them a growth advantage over most of the 0^+ rainbow trout population and resulted in brown trout achieving greater mean size during summer than rainbow trout.

CHAPTER VI

SOCIAL INTERACTIONS BETWEEN JUVENILE BROWN AND RAINBOW TROUT FROM SCOTTS CREEK

6.1 INTRODUCTION

In stream-dwelling juvenile salmonids, competition for space has been substituted for direct competition for food (Chapman 1966). Consequently territoriality is usually strongly expressed in these fish. An essential requirement for a territorial animal is that it must be aggressive toward conspecifics. Aggressive behaviour serves to displace another individual or at least threatens to do so (Manning 1979). In salmonids, aggressive behaviour is a key factor in determining social status of individuals. Social dominance determines feeding opportunities and therefore confers definite benefits on individuals. For example, Kalleberg (1958), Chapman (1962), MacPhee (1961), and Mason and Chapman (1965) have shown that despotic fish in heirarchies and successful territorial fish grow more rapidly than subordinates or refugees. Larger size and prior residence have a marked positive effect on dominance (Noakes 1978). Chapman (1962) suggested that downstream drift of coho salmon fry in some Oregon streams was caused by aggressive behaviour of residents, the emigrants often being socially unsuccessful. LeCren (1961) reported general observations of socially induced downstream emigration in brown trout fry.

Because of their similar ecological requirements stream dwelling juveniles of various salmonids interact socially, e.g., brook and rainbow trout (Newman 1956), brown trout and Atlantic salmon (Kalleberg 1958), coho salmon and steelhead trout (Hartman 1965), brook and cutthroat trout (Griffith 1972), coho and chinook salmon (Stein et al. 1972), coho salmon

and cutthroat trout (Glova 1978), brook trout, rainbow trout, coho and Atlantic salmon (Gibson 1981).

The aim of this study was to determine the potential for interference competition for space between juvenile brown and rainbow trout, through examination of social interactions, particularly in relation to timing of emergence of the two species in Scotts Creek. Field investigations showed that although the temporal pattern of rainbow trout fry emergence completely overlapped that of brown trout, there was considerable separation of the main emergence periods resulting from severe intraspecific interference competition for spawning space between rainbow trout. I therefore investigated the possibility that early emergence by brown fry and by a minority of rainbow fry confers social dominance upon these fish, thus competitively disadvantaging later emerging rainbow fry. Hartman (1965) and Glova (1978) have shown that experimental studies of aggressive activity between species over a habitat gradient can reveal the social status of species in sympatry. This was the approach of the present study. A habitat gradient (a riffle:pool sequence) was included in the experimental design since social dominance by a species can depend on habitat. When species have similar ecological demands and their social dominance is dependent on habitat they may exhibit interactive habitat segregation. Interactive segregation is a magnification of differences in habitat or food selection between species caused by interactions between those species (Nilsson 1965). Such segregation has been demonstrated clearly between juveniles of coho salmon and steelhead trout (Hartman 1965) and coho salmon and cutthroat trout (Glova 1978). Segregation by habitat is one of the most important means by which ecologically similar species partition resources (Schoener 1974). Shifts in habitat use by a species when similar forms are absent thus provide some of the strongest evidence for competition structuring communities (Werner and Hall 1974).

6.2 METHODS

6.2.1 EXPERIMENTAL FACILITY

Social behaviour and microdistribution of underyearling brown and rainbow trout from Scotts Creek were studied at the site in two small observation troughs (see Reimers 1970) (Plate 6.1). Each trough was 2.40 x 0.60 x 0.60m and was divided into a riffle and a pool. Fish were observed through perspex windows large enough to provide an almost complete view of the interior of the troughs. Water from a small tributary of Scotts Creek entered each trough through a 40mm diam. polyethylene pipe. A fine mesh grill in front of, and extending up to the level of, the riffle directed most of the flow upwards. Water then flowed over the riffle, through the pool and out a 10cm x 10cm overflow notch. Water depth was 11cm - 15cm in the riffle and 32cm - 38cm in the pool. The overflow discharge was in the range of 85 - 100 litres.min^{-1}. Based on these flow measurements, the average velocity over the riffle was 1.8 - 2.1 cm.sec^{-1}.

The riffle consisted of gravel overlain on a false bottom that graded into the pool. The bulk of the substrate was natural gravel, in the size range 1cm - 8cm diameter, collected from Scotts Creek. This covered the bottom of the riffle and pool to a depth of about 6cm and 15cm respectively. Fine material (sand and silt) was placed along parts of the margins of both riffle and pool to simulate natural conditions. Overhanging cover was provided by strips of hardboard 45cm x 6cm suspended on the water surface along the margins of both riffle and pool. Grass was attached to these strips and allowed to trail in the water to simulate natural riparian cover.

During the experiments water temperature ranged from 6°C to 17°C.

Plate 6.1 Observation troughs used in the study of social interactions among underyearlings.

Food entered the troughs in the form of natural stream drift and was supplemented daily with stream bottom fauna released in the vicinity of the intake.

A trap was installed below the outfall to catch fish moving downstream. Different sized screens were installed in the overflow notch to retain fish of various sizes in the troughs.

The two troughs were arranged parallel to each other and the intervening area was covered with black polyethylene sheeting to provide a darkened, central observation area.

6.2.2 EXPERIMENTAL PROCEDURE

Fish for the experiments were collected from Scotts Creek by dip netting. They were anaesthetized in 0.003% benzocaine, measured (fork length), weighed damp, then allowed to recover in live boxes before being released into the troughs at night. After two days confinement, to allow fish to recover from handling and to habituate to the trough interior, recently emerged fry were allowed voluntary residence. Each experiment lasted six days. The fish were observed three times daily: in the morning between 0900 and 1030 h., early afternoon between 1330 and 1500 h. and late afternoon between 1630 and 1800 h.. Behavioural observations totalling about six hours were made over the course of each six day experiment. Approximate position, size class and species of each fish was recorded on outline maps of the trough bottom at each observation period; the vertical position of each fish in the pool was also recorded. The aggressive behaviour of all fish in the upstream and downstream halves of the riffle and in the pool was recorded for periods of 5 min, 5 min and 10 min respectively. Sequence of observations in the three sections was chosen randomly. The number of each of the behavioural components of

aggressive encounters (both intra- and interspecific) between the fish were recorded on a set of laboratory counters. The components of agonistic encounters recorded included chase, threat and contact nips, lateral and frontal threat displays, parallel-swimming, circling and intention movement. At the end of each experiment fish were removed by dip netting. All experiments were replicated.

Experiments were divided into two series. Series I was designed to examine general social interactions between recently emerged brown and rainbow fry and the effect of prior residence on these interactions. It was carried out during September when brown fry and early emerging rainbow fry were emerging in Scotts Creek. Sizes of fish used in experiments are summarized in Appendix 2.5. This series was composed of three sets of experiments: observations of microdistribution and aggressive behaviour of fish in 1/ allopatry, 2/ sympatry and 3/ sympatry when one species was given prior residence. Each experiment required 40 fry, with 20 fry of each species in the sympatry tests. The prior residence experiments followed immediately after the allopatry experiments. At the end of each allopatry experiment all fish were removed from the trough. Twenty of these fish were then chosen randomly and immediately released back into the trough. These fish were given at least four hours to recover from handling and re-establish their favoured positions. Twenty naive fry of the other species were then released into the trough at night. Observations commenced the following morning. When less than 20 fry remained after the allopatry tests all were released back into the trough and an equivalent number of naive fry of the other species were introduced.

Series II was designed to examine general social interactions between brown and rainbow fingerlings and between these fish and the much smaller late emerging rainbow fry. The experiments were carried out in November and December with fish of two size classes; recently emerged

rainbow fry, which had emerged late in the emergence period, and larger (early emerged) fingerlings of both species. For sizes of fish, see Appendix 2.5. The series was composed of five sets of experiments: 1/ recently emerged rainbow fry observed in allopatry, 2/ fingerlings of both species in allopatry, 3/ fingerlings of the two species in sympatry, 4/ recently emerged rainbow fry in sympatry with fingerlings of each species and 5/ recently emerged rainbow fry in sympatry with fingerlings of both species together. In experiments with recently emerged fry in allopatry 40 individuals were used, and in those involving fingerlings in allopatry 16 individuals were used. In sympatry experiments involving only fingerlings, eight fish of each species were used and in mixed size class sympatry experiments 30 recently emerged fry and 10 fingerlings were used. These totals were chosen so as to maximize the numbers of experimental fish for statistical analysis while not exceeding the carrying capacity of the troughs. Voluntary residence was allowed for recently emerged fry but not for fingerlings. Escapement of fingerlings was prevented in order to retain sufficient numbers for statistical analysis.

6.2.3 PROCESSING OF DATA

The microdistributions of brown and rainbow trout in the observation troughs were tested statistically by factorial analysis of variance. To standardize the numbers of fish of each species or of each size class in a given habitat, each observation was expressed as a percentage of the total fish of each species or size class present. The data were then transformed by the arcsine transformation (Sokal and Rohlf 1969). The statistical analysis was designed to determine if the differences in microdistribution were significant 1/ between species and

size classes in allopatry, 2/ between species and size classes in sympatry, 3/ within species and size classes between allopatric and sympatric tests, 4/ between species when one species was given prior residence, and 5/ within species between sympatric and prior residence sympatric tests.

For behavioural analysis intra- and interspecific interactions were treated separately. For intraspecific interactions, species individual components of aggression were summed and divided by the number of fish observed in order to standardize fish density. The rate of aggression evident in interspecific interactions was dependent on densities of both species present. To make the rate independent of density, the relative proportions of the two species were equalized. This was achieved by:

$$T = T_o \frac{A}{B}$$

where T_o is the sum of a species individual components of aggression, T is the corrected sum, A is the number of that species observed and B is the number of the other species observed. The interspecific rate of aggression R, could then be calculated as:

$$R = \frac{T}{A}$$

These two equations were condensed to:

$$R = \frac{T_o}{B}$$

In this form inter- and intraspecific rates of aggression were directly comparable. Combining intra- and interspecific rates gave a comparative

measure of species rate of aggression. Most of the data were tested statistically by Mann-Whitney U (Sokal and Rohlf 1969) but wherever applicable Students t was used. Statistical analysis of behavioural components of aggression was done using Chi-square.

6.3 RESULTS

6.3.1 GENERAL

During the first day of each experiment naive fish showed a gradual spacing out after initial aggregations in the downstream half of the riffle and riffle:pool interface. Recently emerged rainbow fry showed a stronger tendency to invade the upstream half of the riffle than did recently emerged brown fry. The fish initially exhibited exploratory behaviour (roaming widely in the trough). This gradually subsided over the first two days as individual territories and dominance hierarchies became established and stabilized. Because of this initial period of instability in social organization, observations made during the first two days were excluded from analysis. This procedure did not bias the results against either species, since both showed little change in pattern of habitat partitioning with time and general species trends in social interactions with time were similar.

In the analysis of microdistribution I assumed that the microdistributions recorded at each observation period were independent of each other and therefore could be treated as true replicates in the analysis of variance. I tested the validity of this assumption by one way analyses of variance carried out on the microdistribution results for recently emerged brown and rainbow trout in allopatry, comparing between days and between observation times. This procedure established that no

trends existed between days or observation times.

There were no significant differences between microdistribution or aggressiveness of early emerging rainbow fry used in Series I and late emerging rainbow fry used in Series II. Therefore comparisons made between the two sets of experiments are valid.

6.3.2 MICRODISTRIBUTION

6.3.2.1 RECENTLY EMERGED FRY

The microdistributions of recently emerged brown and rainbow fry recorded in both allopatry and sympatry showed distinct interspecific differences (Fig. 6.1). In allopatry and in sympatry both species significantly preferred the riffle. This preference was significantly greater in rainbows than in browns (Tables 6.1 and 6.2). In allopatry neither species showed a significant difference in preference between the two halves (upstream and downstream) of the riffle. However, a significantly higher proportion of rainbow fry utilized the upstream riffle than did brown fry (Tables 6.1 and 6.2). In allopatry brown fry showed no difference in preference between the upper and lower pool, whereas rainbow fry showed a significant preference for the pool surface (Tables 6.1 and 6.2).

In general, brown fry exhibited a closer association with the substrate than did rainbow fry. As also reported by Kalleberg (1958), brown fry often rested on the substrate with their pectoral fins acting as hydrodynamic anchors, rising occasionally to intercept food items or to attack an intruder. In contrast, rainbow fry usually were observed up in the water column swimming against a current. In calmer waters (e.g., as in the pool) rainbows often established large loose territories, over

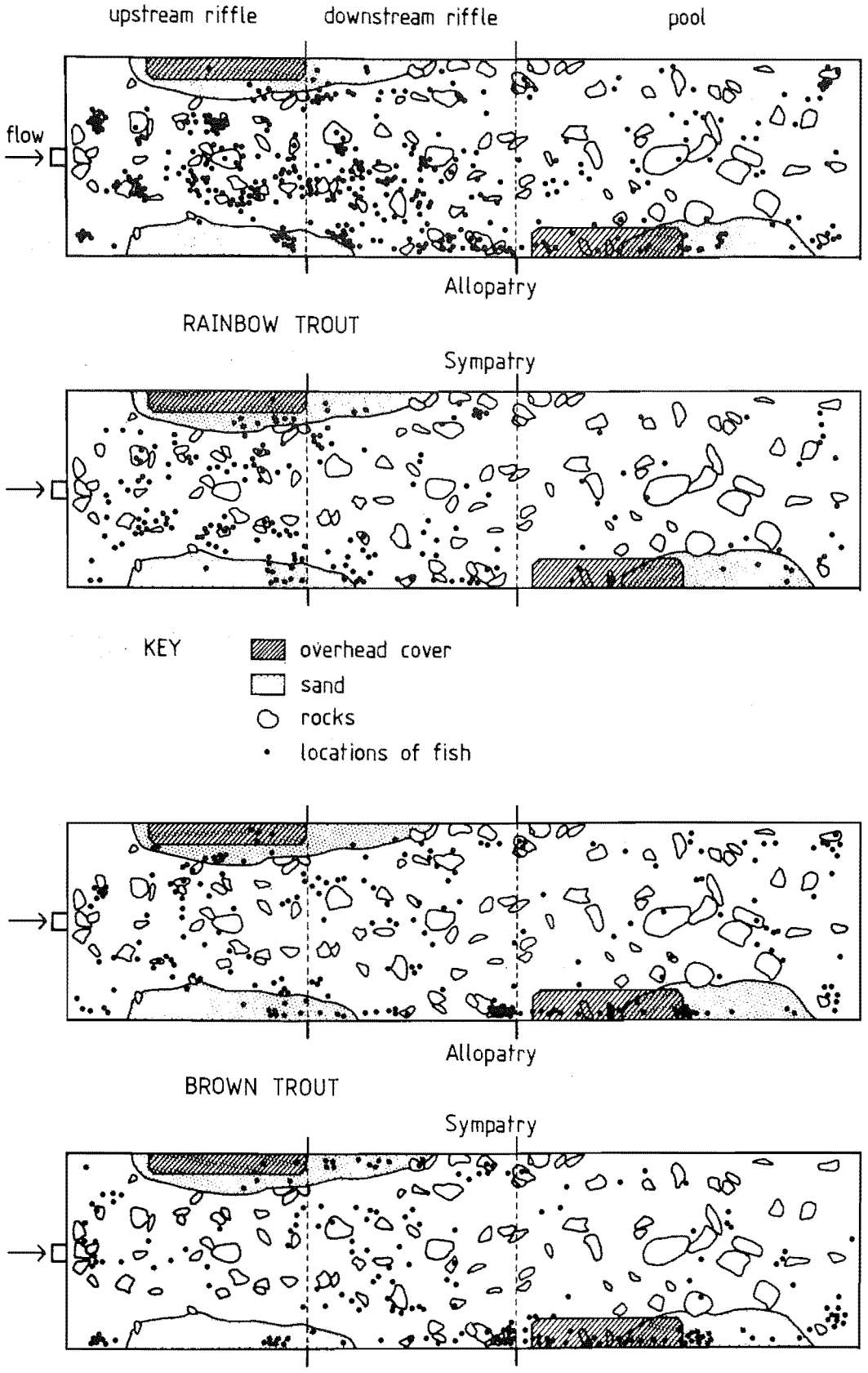


Figure 6.1 Cumulative plots of microdistributions of recently emerged brown and rainbow fry in allopatry and in sympatry.

Table 6.1 Mean proportions (± S.E., n = 24) of recently emerged brown fry (B. fry) and rainbow fry (R. fry) in the different categories of microhabitat in each experiment of series I.

		Allopatry	Sympatry	Sympatry R. fry with prior residence	Sympatry B. fry with prior residence
Rainbow fry	riffle	0.786 ± 0.0131	0.804 ± 0.0244	0.794 ± 0.0201	0.700 ± 0.0284
	upstream	0.407 ± 0.0150	0.513 ± 0.0276	0.511 ± 0.0198	0.383 ± 0.0304
	downstream	0.359 ± 0.0151	0.291 ± 0.0253	0.283 ± 0.0135	0.317 ± 0.0203
	pool	0.224 ± 0.0121	0.197 ± 0.0247	0.208 ± 0.0203	0.294 ± 0.0323
	upper	0.144 ± 0.0098	0.158 ± 0.0225	0.133 ± 0.0202	0.184 ± 0.0292
	lower	0.079 ± 0.0091	0.039 ± 0.0085	0.075 ± 0.0185	0.116 ± 0.0170
Brown fry	riffle	0.665 ± 0.0192	0.614 ± 0.0258	0.572 ± 0.0340	0.564 ± 0.0259
	upstream	0.323 ± 0.0174	0.224 ± 0.0277	0.311 ± 0.0325	0.226 ± 0.0292
	downstream	0.340 ± 0.0184	0.369 ± 0.0237	0.259 ± 0.0329	0.338 ± 0.0364
	pool	0.335 ± 0.0192	0.386 ± 0.0258	0.414 ± 0.0348	0.435 ± 0.0259
	upper	0.173 ± 0.0178	0.178 ± 0.015Q	0.177 ± 0.0226	0.235 ± 0.0205
	lower	0.162 ± 0.0172	0.209 ± 0.0211	0.242 ± 0.0341	0.212 ± 0.0201

Table 6.2 Variables

Microhabitat - R = riffle, P = pool, Ru = upstream riffle, Rd = downstream riffle, Pu = upper pool, Pl = lower pool.

Experiment type - A = allopatry, S = sympatry, R.pr = sympatry when rainbow fry had prior residence, B.pr = sympatry when brown fry had prior residence.

Two F values (i.e. - / -) means a significant interaction effect was present in the overall design. Consequently, each habitat was tested separately.

Resultant F values are given in order of experimental description i.e. R/P = F=R/F=P N.B. this measures difference in utilization of each habitat and not differences in habitat preference.

* significant heteroscedasticity between the data sets make this significant result dubious.

Table 6.2 Comparison of F values ($P < 0.05$ underlined, $P < 0.01$ double underlined) (d.f.) from factorial analyses of variance of the brown and rainbow trout tests in Series I.

	Between species		Within species	
	Allopatry	Sympatry	Rainbow	Brown
R/P	24.18/22.78 (1,46)	25.73/ (1,46)	663.77 (1,46)	129.98 (1,46)
Ru/Rd	13,76/0.70 (1,46)		0.68 (1,2)	0.07 (1,2)
Pu/Pl	13.63 (1,2)		21.25 (1,46)	0.09 (1,2)
R/P x A/S			0.05 (1,92)	2.34 (1,46)
Ru/Rd x A/S			2.26/5.03(1,2)(1,46)	6.82/0.29(1,46)(1,2)
Pu/Pl x A/S			*7.97 (1,2)	1.68 (1,2)
R/P x S/R.pr			0.02 (1,184)	0.02 (1,184)
Ru/Rd x S/R.pr			0.94 (1,2)	1.27 (1,2)
Pu/Pl x S/R.pr			0.01 (1,2)	0.01 (1,2)
R/P x S/B.pr			0.05 (1,2)	0.05 (1,2)
Ru/Rd x S/B.pr			3.03 (1,2)	1.65 (1,2)
Pu/Pl x S/B/pr			8.61 (1,2)	2.78 (1,90)

which they continuously roamed, near the surface. Newman (1956) described a similar contrast in behaviour between brook and rainbow trout.

In contrast with microdistributions in allopatry, in sympatry, interactive segregation within the riffle resulted in a significant reduction in proportional utilization of the downstream riffle by rainbow fry and of the upstream riffle by brown fry (Fig. 6.1, Tables 6.1 and 6.2). Reduction in utilization of the upstream riffle by brown fry in sympatry resulted in the apparent slight habitat shift from the riffle to the pool recorded for that species (Table 6.1). The reverse trend recorded for rainbow trout (Table 6.1) results from a real reduction in numbers of rainbow fry utilizing the pool (Fig 6.1). However, neither of these slight habitat shifts were statistically significant (Table 6.2).

Since food in the form of natural invertebrate drift entered the troughs via the inflow pipes it would be advantageous for fish to occupy the upstream riffle, and dominant fish would be expected to colonize this microhabitat. Slaney and Northcote (1974) studied aspects of rainbow fry behaviour in laboratory channels where food was introduced via the inflow, and observed that territorial fry in the upstream sections of the channel appeared to be much more dominant than those further downstream. Although the size range of recently emerged fry used in my experiments was narrow, larger fish were dominant and most of the larger rainbow fry held stations in the upstream riffle.

6.3.2.2 PRIOR RESIDENCE

Prior residence did not significantly affect the pattern of habitat partitioning between the species. For most habitat pairs, comparisons between tests in sympatry and tests in sympatry when either species was given prior residence revealed no significant differences in

species microdistributions (Tables 6.1 and 6.2). The significant change in microdistribution of rainbow fry within the pool when brown fry were given prior residence (Table 6.2), was due to an overall slight increase in utilization of the pool, in particular the lower pool by rainbow fry (Table 6.1). However, the significance of this result is questionable since it is based on very small samples, i.e. usually less than three or four fish in each microhabitat per observation. An associated reduction in utilization of the upstream riffle by rainbow fry, although not significant, suggests that dominance of rainbow fry in this microhabitat might have been weakened by prior residence by brown fry. Braddock (1949) showed that prior residence increases the potential for dominance in individual Platypoecilus maculatus. If this had occurred in brown fry, and resulted in rainbow fry being denied access to space in the upstream riffle, I would have expected to see a corresponding higher utilization of the upstream riffle by brown fry than was observed when they were denied prior residence. That the results do not show this (Table 6.1) may be due to an interference with this experiment. One of the replicates was interrupted soon after it began by a large galaxiid (Galaxias brevipinnis) (approximately 12cm) which entered the trough via the inflow. The presence (for one night) of this fish resulted in the emigration of most of the fry from the trough. Although the galaxiid was removed and the fry released back into the trough, the brown fry never regained their original home stations and the rainbow fry rapidly colonized the upstream riffle. In the other replicate, a higher number of brown fry remained in the upstream riffle until near the end of the test, when they appeared to be displaced by increasing numbers of rainbow fry. The mean proportion of brown fry in the upstream riffle in this replicate was 0.271 but was not significantly greater than the mean proportion, calculated from both replicates, recorded in sympatry with no prior residence (i.e., 0.224).

The effect of prior residence on dominance can gradually diminish with time and other factors may predominate as the intruder becomes more familiar with the area (Braddock 1949). With this possibility in mind I analysed the results of both prior residence experiments to determine if species microdistribution did change significantly with time during the experiments. Comparison between mean species microdistribution for the first two days of each experiment and the remaining days revealed slight changes in microdistribution with time, particularly in brown fry given prior residence (Table 6.3). However, only one of these changes was statistically significant (Table 6.4). The significant change in microdistribution of the rainbow fry within the pool was caused by an overall increase in utilization of the pool, in particular the lower half of the pool, by that species with time. However small sample sizes recorded within the pool require that the significance of this result be viewed with suspicion. In the presence of introduced rainbow fry, brown fry given prior residence exhibited a slight shift downstream from the upper riffle into the lower riffle and pool with time (Table 6.3). Species microdistributions changed least with time when rainbow fry had prior residence. There is some evidence to suggest that prior residence by rainbow fry induced displacement of naive brown fry from the troughs, since in this test more (although not significantly more) brown fry emigrated from the troughs than in the other sympatry tests (Fig. 6.2).

6.3.2.3 FINGERLINGS

In contrast with recently emerged fry, microdistributions of fingerlings were characterized by a general lessening in habitat preference (Table 6.5, Fig. 6.3). The strong preference for the riffle

Table 6.3 Comparison of mean proportions of recently emerged brown and rainbow fry in the different categories of microhabitat between the first two days and the remaining days in the prior residence experiments.

			Sympatry R.fry with prior residence		Sympatry B.fry with prior residence	
			First two days	Remaining days	First two days	Remaining days
	riffle		0.822 ± 0.0206	0.794 ± 0.0201	0.765 ± 0.0408	0.700 ± 0.0284
		upstream	0.483 ± 0.0236	0.511 ± 0.0198	0.341 ± 0.0371	0.383 ± 0.0304
rainbow fry		downstream	0.340 ± 0.0218	0.283 ± 0.0135	0.424 ± 0.0425	0.317 ± 0.0203
	pool		0.176 ± 0.0211	0.208 ± 0.0203	0.207 ± 0.0385	0.294 ± 0.0323
		upper	0.116 ± 0.0191	0.133 ± 0.0202	0.120 ± 0.0256	0.184 ± 0.0292
		lower	0.061 ± 0.0196	0.075 ± 0.0185	0.087 ± 0.0242	0.116 ± 0.0170
	riffle		0.581 ± 0.0337	0.572 ± 0.0340	0.613 ± 0.0266	0.564 ± 0.0259
		upstream	0.283 ± 0.0357	0.311 ± 0.0325	0.313 ± 0.0319	0.226 ± 0.0292
brown fry		downstream	0.297 ± 0.0292	0.259 ± 0.0329	0.299 ± 0.0335	0.338 ± 0.0364
	pool		0.417 ± 0.0327	0.414 ± 0.0348	0.384 ± 0.0305	0.435 ± 0.0259
		upper	0.197 ± 0.0202	0.177 ± 0.0226	0.201 ± 0.025	0.235 ± 0.0205
		lower	0.221 ± 0.0261	0.242 ± 0.0341	0.197 ± 0.0248	0.212 ± 0.0201

R.fry = rainbow fry

B.fry = brown fry

Table 6.4 F values (P <0.05 underlined) (d.f.) for comparison between the first two days and the remaining days in each habitat pair in the prior residence experiments.

	R. fry with prior residence		B. fry with prior residence	
	R. fry	B. fry	R. fry	B. fry
R/P	0.01 (1,152)	0.01 (1,152)	0.09 (1,2)	0.09 (1,2)
Ru/Rd	1.63 (1,2)	1.63 (1,2)	2.10 (1,2)	2.10 (1,2)
Pu/Pl	0.09 (1,2)	0.09 (1,2)	*4.55(1,2)	1.68 (1,2)

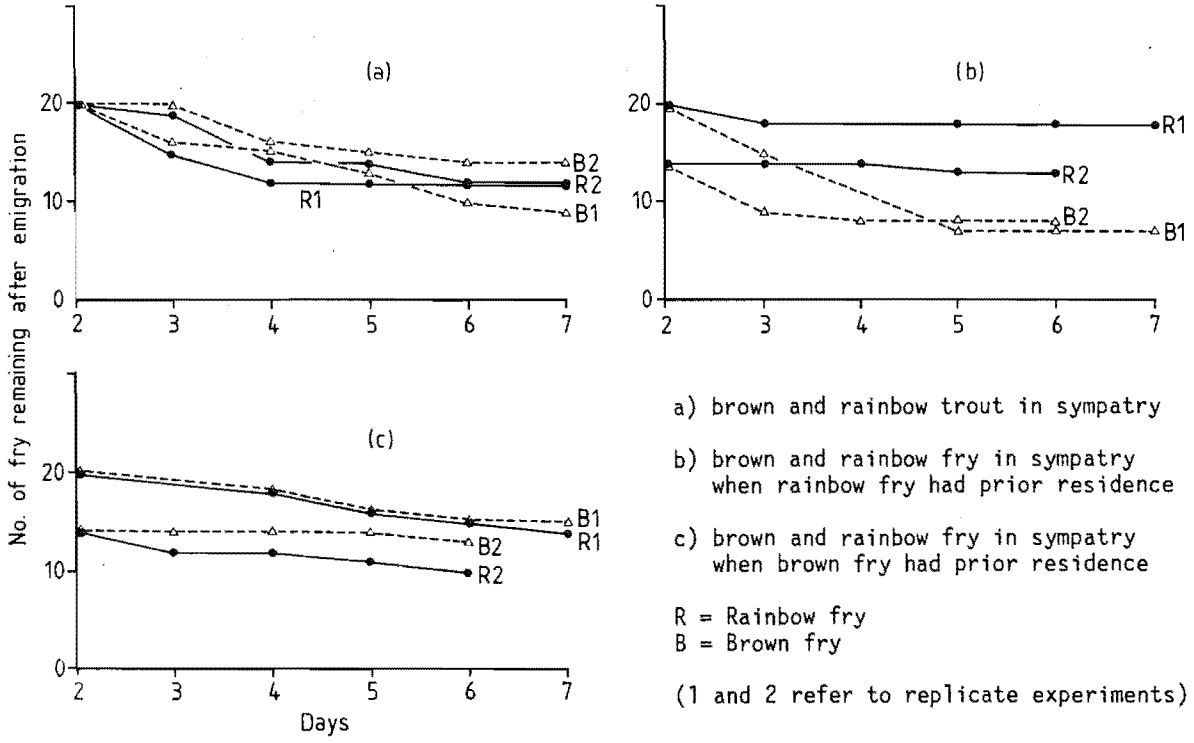


Figure 6.2 Numbers of resident fry remaining, after emigration, in the observation troughs during prior residence and non-prior residence sympatry tests of Series I. (Replicates 1 and 2)

Table 6.5 Mean proportions (± S.E., n = 24) of fingerling brown (B. fing.) and rainbow (R.fing.) trout and recently emerged rainbow fry (R. fry) in the different categories of microhabitat in each experiment of Series II.

		Allopatry	Sympatry		
			R.fing. x B.fing.	R.fing. x R.fry	B.fing. x R.fry
Rainbow fingerlings	riffle	0.615 ± 0.0298	0.491 ± 0.0336	0.737 ± 0.0470	
	upstream	0.344 ± 0.0319	0.158 ± 0.0281	0.453 ± 0.0435	
	downstream	0.270 ± 0.0176	0.333 ± 0.0391	0.285 ± 0.0331	
	pool	0.385 ± 0.0298	0.502 ± 0.0327	0.262 ± 0.0470	
	upper	0.201 ± 0.0289	0.306 ± 0.0328	0.178 ± 0.0362	
	lower	0.185 ± 0.0321	0.195 ± 0.0357	0.177 ± 0.0407	
Brown fingerlings	riffle	0.510 ± 0.0305	0.582 ± 0.0251		0.595 ± 0.0276
	upstream	0.236 ± 0.0300	0.328 ± 0.0272		0.338 ± 0.0156
	downstream	0.274 ± 0.0267	0.254 ± 0.0294		0.256 ± 0.0243
	pool	0.491 ± 0.0305	0.418 ± 0.0251		0.405 ± 0.0275
	upper	0.355 ± 0.0273	0.287 ± 0.0239		0.270 ± 0.0281
	lower	0.136 ± 0.0202	0.132 ± 0.0254		0.136 ± 0.0216
Rainbow fry	riffle	0.830 ± 0.0258		0.818 ± 0.0099	0.857 ± 0.0131
	upstream	0.430 ± 0.0253		0.411 ± 0.0162	0.548 ± 0.0275
	downstream	0.400 ± 0.0170		0.409 ± 0.0135	0.310 ± 0.0211
	pool	0.170 ± 0.0258		0.180 ± 0.0096	0.161 ± 0.0193
	upper	0.098 ± 0.0160		0.123 ± 0.0081	0.096 ± 0.0104
	lower	0.073 ± 0.0149		0.057 ± 0.0084	0.047 ± 0.0072

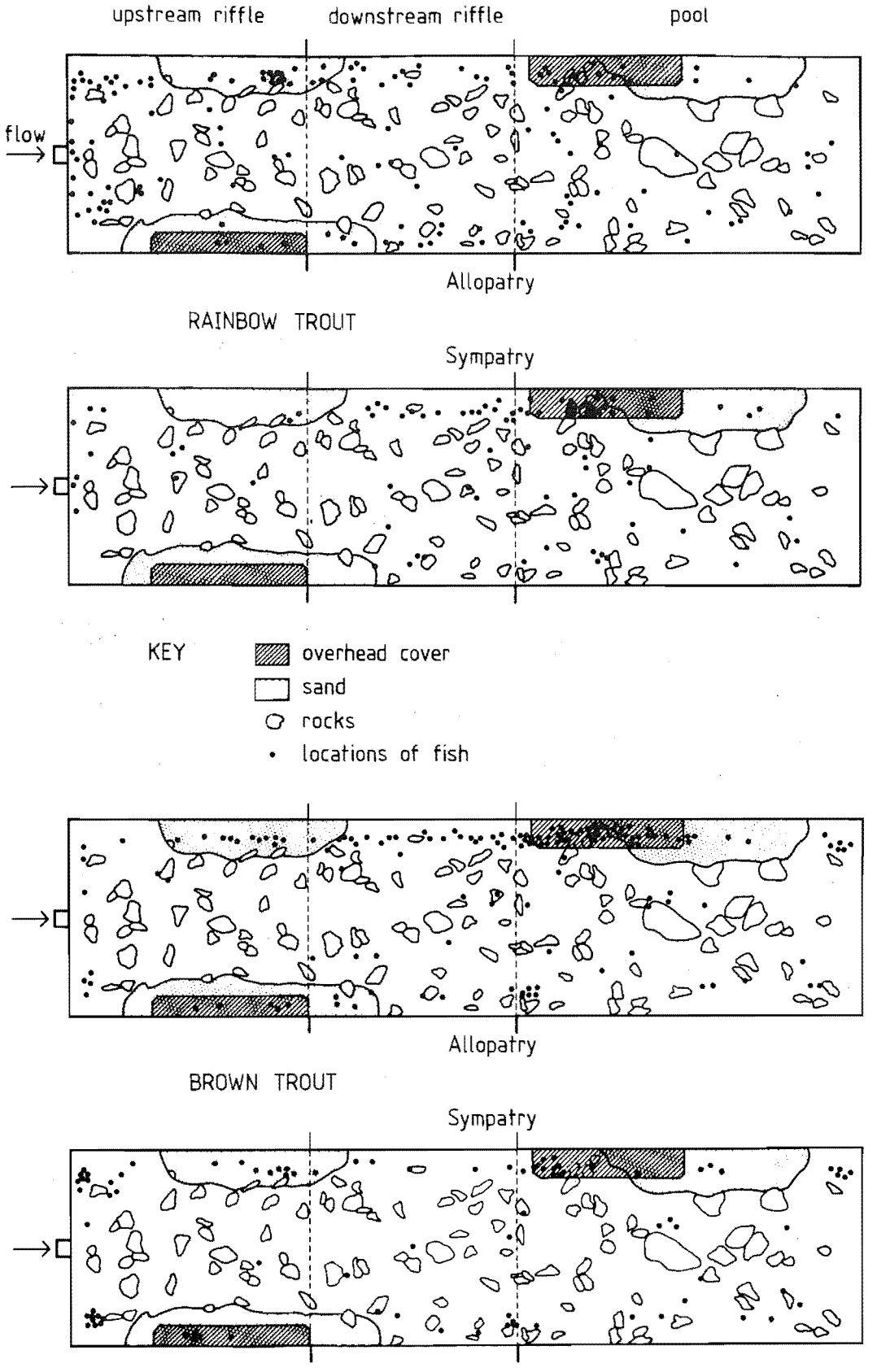


Figure 6.3 Cumulative plots of microdistributions of brown and rainbow fingerlings in allopatry and in sympatry.

habitat exhibited by fry was not observed in fingerlings. However, I consider that water velocity was a limiting factor in not providing an adequate deep swift habitat for the larger juveniles. Therefore, microdistributions of fingerlings recorded in these troughs might not accurately reflect those in a natural stream.

Brown fingerlings in sympatry, but not in allopatry, showed a significant preference for the riffle ($P < 0.01$) (Table 6.5). However, microdistribution of brown fingerlings in sympatry was not significantly different to that in allopatry. This apparent inconsistency arose because in the comparison between microdistribution in allopatry and that in sympatry, a significant difference between allopatry replicate experiments precluded pooling of the data sets. This lowered the degrees of freedom thereby de-sensitizing the test. For the same reason, the apparent preference of rainbow fingerlings for the riffle in allopatry (Table 6.5) was also not significant. In sympatry, rainbow fingerlings were excluded from the upstream riffle by three or four dominant brown trout that aggressively defended this area. Hence, rainbow fingerlings exhibited significantly lower utilization of the upstream riffle in sympatry than in allopatry, whereas utilization of this microhabitat by brown fingerlings was similar in sympatric and allopatric trials (Table 6.6, Fig. 6.3).

Within the pool, the surface was preferred by both species in both allopatry and sympatry, although this preference was statistically significant only for brown fingerlings (Tables 6.5 and 6.6). Brown fingerlings exhibited significantly higher utilization of the pool surface than did rainbow fingerlings (Table 6.6).

Overhead cover in the pool was commonly used by fingerlings, particularly those of brown trout (Fig. 6.3).

Table 6.6 Comparison of F values (P <0.05 underlined, P <0.01 double underlined) (d.f.) from factorial analysis of variance of the brown and rainbow fingerlings and rainbow fry tests in Series II.

	Between species	Within species		
	Allopatry	Rainbow fingerlings	Rainbow fry	Brown fingerlings
R/P x fing.	0.00 (1,2)	3.82 (1,2)	187.25 (1,46)	0.20 (1,46)
Ru/Rd x fing.	*	0.47 (1,2)	0.80 (1,46)	0.71 (1,46)
Pu/Pl x fing.	14.33/0.60 (1,46)	0.22 (1,46)	1.06 (1,46)	35.97 (1,46)
R/P x fing. x A/S		0.01 (1,2)		0.00 (1,2)
Ru/Rd x fing. x A/S		20.11/1.11 (1,46)		1.73 (1,2)
Pu/Pl x fing. x A/S		0.05 (1,184)		0.05 (1,184)
R/P x R.fing./fry x A/S			0.00 (1,92)	
Ru/Rd x R.fing./fry x A/S			0.04 (1,92)	
Pu/Pl x R.fing./fry x A/S			1.61 (1,92)	
R/P x B.fing. x fry x A/S			0.00 (1,2)	4.32/ (1,46)
Ru/Rd x B.fing. x fry x A/S			0.33 (1,2)	10.83/0.16 (1,46)
Pu/Pl x B.fing. x fry x A/S			0.00 (1,2)	2.82 (1,2)

See variables key Table 6.2 fing. = fingerlings, R.fing. = rainbow fingerlings, B.fing. = brown fingerlings.

* This result is excluded since significant interaction effects between the replicates of this experiment are included in the main effect of the ANOVA. However, a significant difference between the species is unlikely since both show no preference for either microhabitat.

6.3.2.4 HABITAT SHARING BETWEEN RECENTLY EMERGED RAINBOW FRY AND FINGERLINGS

The presence of fingerlings of either species did not significantly affect the microdistribution or emigration of recently emerged rainbow fry (Tables 6.5 and 6.6, Fig. 6.4).

Brown fingerlings exhibited significantly higher utilization of the riffle, in particular the upstream riffle, in sympatry with rainbow fry than in allopatry (Table 6.6). This result is surprising since I would not expect recently emerged fry to affect the microdistribution of much larger juveniles. This anomalous result could be due to density differences of fingerlings between the tests. In sympatric experiments where the two size classes were mixed, a lower number of fingerlings was used than in allopatric experiments. The number of fingerlings used in the allopatric experiments might have exceeded the carrying capacity of the troughs. Since these fingerlings were denied voluntary residence any excess fish would be forced into less preferred habitats. This situation could mask microhabitat preferences that otherwise would be apparent under conditions of lower density of fingerlings, for example as in the sympatric experiments.

Microdistributions of rainbow fingerlings when mixed with recently emerged fry are not included in Tables 6.5 and 6.6; small sample sizes caused by the escape of these fish from the observation troughs resulted in unacceptably high variance in the data. Experiments involving brown and rainbow fingerlings and recently emerged rainbow fry in sympatry gave similar results to those described above, i.e., the presence of fingerlings did not affect the microdistribution of recently emerged fry. Small sample sizes of fingerlings also precluded the inclusion of these data in the tables.

Although fingerlings and fry did not segregate between

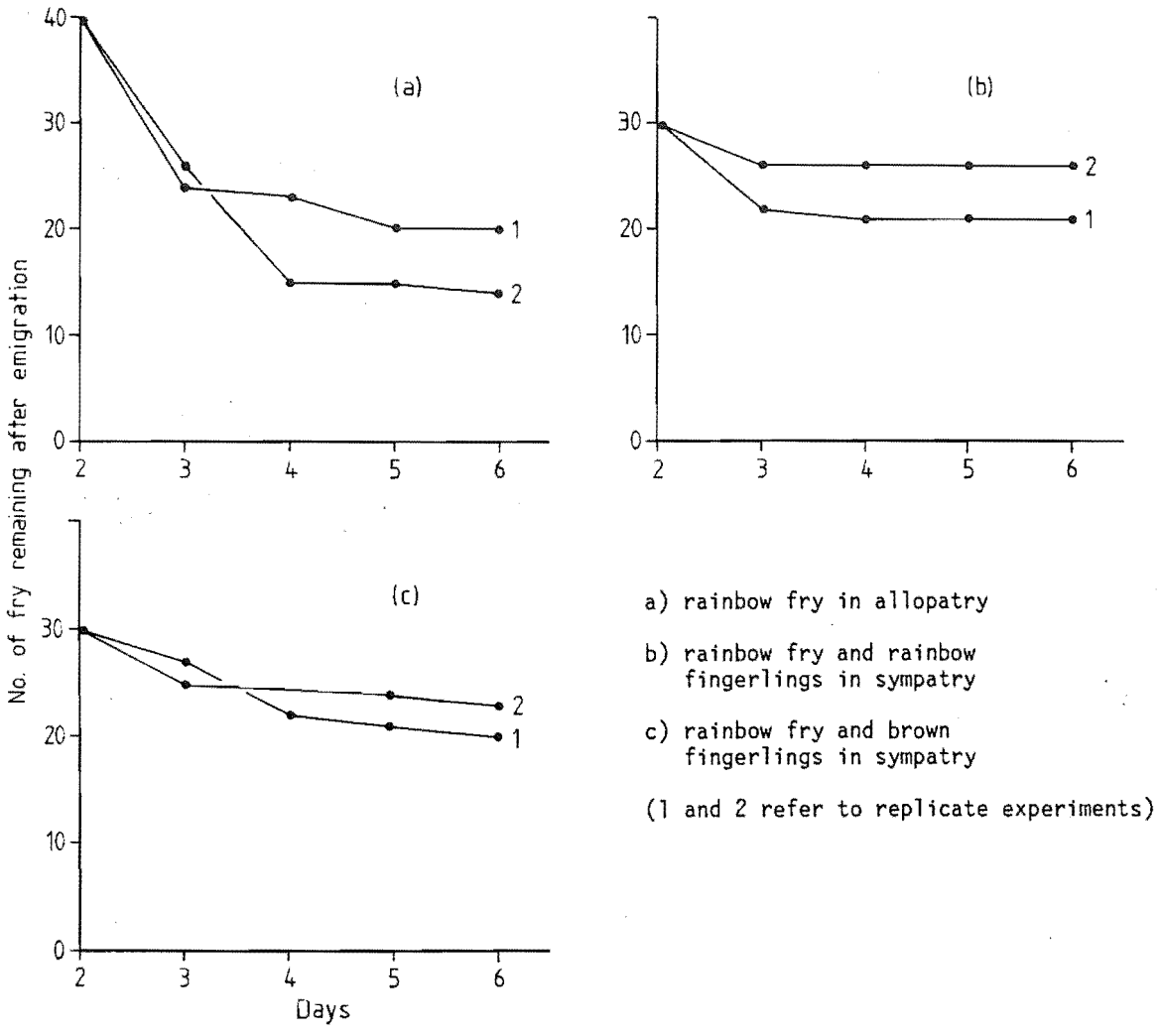


Figure 6.4 Number of resident rainbow fry remaining, after emigration, in the observation troughs during the mixed size class sympatry tests and during the test with rainbow fry in allopatry in Series II. (Replicates 1 and 2).

respective microhabitat pairs they did appear to segregate within the upstream riffle. Most fingerlings took up stations around the outside edges of the upstream riffle where water velocities were highest, whereas recently emerged rainbow fry congregated in the middle where water velocities appeared generally lower.

6.3.3 AGGRESSIVE BEHAVIOUR

6.3.3.1 BEHAVIOURAL COMPONENTS OF AGGRESSION

Underyearling brown and rainbow trout used similar aggressive behavioural components in agonistic encounters. These behavioural components are fairly consistent among juvenile stream-dwelling Salmonidae and have been described by previous workers: chasing, threat and contact nips and intention movement (Hartman 1965, Mason 1969), lateral and frontal threat displays (Fabricius 1953, Kalleberg 1958, Chapman 1962), and parallel-swimming, circling and biting (Mason 1969).

The most prolonged bouts of fighting were recorded between fish of similar size, usually early in the formation of territories and social hierarchies.

Individual components of aggressive behaviour were expressed as a percentage of the pooled data for each species. This allowed for comparisons of frequency of use of individual components of aggression within and between species (Table 6.7). The most frequently used components of aggression by both brown and rainbow trout of either size class were those of chase, nip and lateral display. Non-contact behaviours (i.e., threat displays) were used significantly more frequently by brown trout, in contrast to the predominant nipping

Table 6.7 Percent frequency of individual behavioural component use, and tests of significance (Chi-square * = 0.05%, ** = 0.01%) between the species and size classes.

	Percentage							
	R.fry	R.fing.	B.fry	B.fing.	R.fry x B.fry	R.fing. x B.fing.	R.fry x R.fing.	B.fry x B.fing.
Chase	29.0	29.0	32.0	28.1	NS	NS	NS	*
Nip	42.2	27.7	23.4	18.0	**	**	**	**
Lateral display	19.6	25.0	26.9	36.9	**	**	**	**
Intention movement	7.1	11.5	13.2	6.8	**	**	**	**
Frontal display	0.9	6.0	4.2	9.5	**	**	**	**
Parallel swim	0.1	0.2	0.2	0.5	NS	NS	NS	NS
Circling	1.2	0.6	0.2	0.2	*	NS	**	NS

behaviour of rainbow trout. Hartman (1963) reported that young brown trout use more non-display than display forms of aggression when in faster water. This was not observed for brown trout in the present study. However, in recently emerged rainbow fry the differences in proportions of non-display (intention movements excluded) over display forms of aggression were significantly higher in the riffle than in the pool ($P< 0.01$, Chi-square). Absence of this difference in fingerlings, in the present study, might in part have been due to the lack of a sufficiently wide range of water velocities in the observation troughs. In both species, fingerlings used significantly more display than non-display forms of aggression compared with recently emerged fry ($P<0.01$, Chi-square).

Individual components of aggression can be characterized according to their apparent offensive or defensive function. Kleenleyside and Yamamoto (1962) concluded that high attack tendencies were expressed by chasing, nipping and to a lesser extent by the frontal display. Therefore, these components have an offensive function, whereas the lateral display is associated with high escape tendencies and therefore has a defensive function. A comparison of frequencies of offensive and defensive components of aggression between intra- and interspecific encounters should reveal the more aggressive species in sympatric experiments. In tests with recently emerged brown and rainbow fry in sympatry (Table 6.8), a significantly higher frequency of chasing and lower frequency of lateral display exhibited by rainbows, in interspecific than in intraspecific interactions, indicates that they were the more aggressive species. In the sympatric test with fingerlings this role was reversed. Brown trout were the more aggressive species, as indicated by the significantly higher frequency of chasing and nipping and the lower frequency of lateral display in interspecific than in intraspecific interactions. Rainbow fingerlings exhibited opposite trends

Table 6.8 Comparison of percent frequency of individual agonistic behavioural components between intra- and interspecific interactions within each size class for experiments with brown and rainbow fry and fingerlings in sympatry. (Chi-square significance levels * = 0.05%, ** = 0.01%).

	R.fry			B.fry			R.fing.			B.fing.		
	intra-	inter-		intra-	inter-		intra-	inter-		intra-	inter-	
Chase	26.6	34.5	*	28.7	26.9	NS	30.3	20.4	**	24.7	35.1	**
Nip	40.4	45.8	NS	20.7	19.2	NS	34.3	17.8	**	19.5	24.0	*
Lateral display	21.2	10.3	**	33.3	32.3	NS	20.8	41.1	**	40.1	27.1	**
Intention movement	10.3	8.4	NS	10.3	17.4	NS	8.4	11.5	NS	6.7	7.6	NS
Frontal display	0.4	0.5	NS	5.7	3.6	NS	4.8	8.6	*	8.5	6.0	NS
Parallel swim	0.4	0	NS	1.1	0	NS	0.3	0.3	NS	0.3	0.1	NS
Circling	0.7	0.5	NS	0	0.6	NS	1.1	0.3	NS	0.2	0.1	NS

Table 6.9 Comparison of percent frequency of individual agonistic behavioural components between within-size-class and between-size-class interactions for each size class in experiments with brown and rainbow fingerlings in sympatry with rainbow fry. (Chi-square significance levels * = 0.05%, ** = 0.01%).

	Rainbow fingerlings x rainbow fry						Brown fingerlings x rainbow fry					
	R.fing.			R.fry			B.fing.			R.fry		
	within-	between-		within-	between-		within-	between-		within-	between-	
Chase	25.1	36.7	**	25.8	13.5	**	26.5	33.3	*	23.7	0	**
Nip	33.0	38.5	NS	32.6	18.8	**	16.4	22.9	*	30.3	0	**
Lateral display	25.5	5.9	**	36.3	57.3	**	37.8	10.0	**	40.6	97.8	**
Intention movement	9.1	18.3	**	4.2	9.4	*	9.2	10.0	NS	4.4	2.2	NS
Frontal display	5.0	0.6	**	0.6	1.0	NS	9.7	4.6	**	0.7	0	NS
Parallel swim												
Circling												

in frequencies of these components. In sympatric tests involving the two size classes, fingerlings were more aggressive than fry (Table 6.9). Fingerlings of both species also showed significantly lower frequencies of frontal display in interactions between size classes, than those within size classes. Brown fingerlings exhibited higher chase and nip frequencies in between-size-class, compared with within-size-class, interactions. This situation, although indicating behavioural dominance of brown fingerlings, may also reflect an intent by some individuals to prey on recently emerged rainbow fry, since on two occasions brown fingerlings were seen to eat small rainbow fry.

6.3.3.2 RATES OF AGGRESSIVE ACTIVITY

As recently emerged fry, rainbow trout were significantly more aggressive than brown trout as measured by pooled species rates of aggression (Table 6.10). However, as fingerlings, brown trout were significantly more aggressive than rainbow trout. In both species fingerlings were significantly more aggressive than recently emerged fry ($P < 0.01$). Increase in aggression with larger size was much more pronounced in browns than in rainbows and resulted in the switching of social dominance between the species.

Rate of aggression in rainbow trout, but not in brown trout, was dependent on microhabitat (Table 6.10). Recently emerged rainbow fry were most aggressive in the upstream riffle. This was the only microhabitat in which rainbow fry were significantly more aggressive than brown fry (Table 6.10). Rainbow fingerlings were more aggressive in the riffle than in the pool. However, in all microhabitats brown fingerlings were significantly more aggressive than rainbow fingerlings (Table 6.10).

Mixing the species had the overall effect of increasing

Table 6.10 Mean species rates of aggression (aggressive encounters/fish/5 min.) ± S.E. for the two size classes in each microhabitat, and U test significance levels (* = 0.05%, ** = 0.01%) for comparisons within species between microhabitats and between species within microhabitats.

	R. fry	R. fing.	B. fry	B. fing.	BETWEEN SPECIES R.fry x B. fry	BETWEEN SPECIES R. fing. x B. fing.
Pooled total all habitats	1.81±0.194	3.38±0.315	0.92±0.143	5.93±0.382	**	**
Riffle	2.34±0.259	4.28±0.442	0.90±0.141	6.60±0.608	**	**
upstream riffle	3.09±0.463	3.71±0.583	0.76±0.129	6.80±0.973	**	**
downstream riffle	1.51±0.267	4.62±0.626	1.05±0.204	6.24±0.656	NS	*
Pool	1.31±0.272	2.64±0.435	0.95±0.249	5.24±0.449	NS	**
Riffle/pool	**	**	NS	NS		
upstream/ downstream riffle	**	NS	NS	NS		
	WITHIN SPECIES					

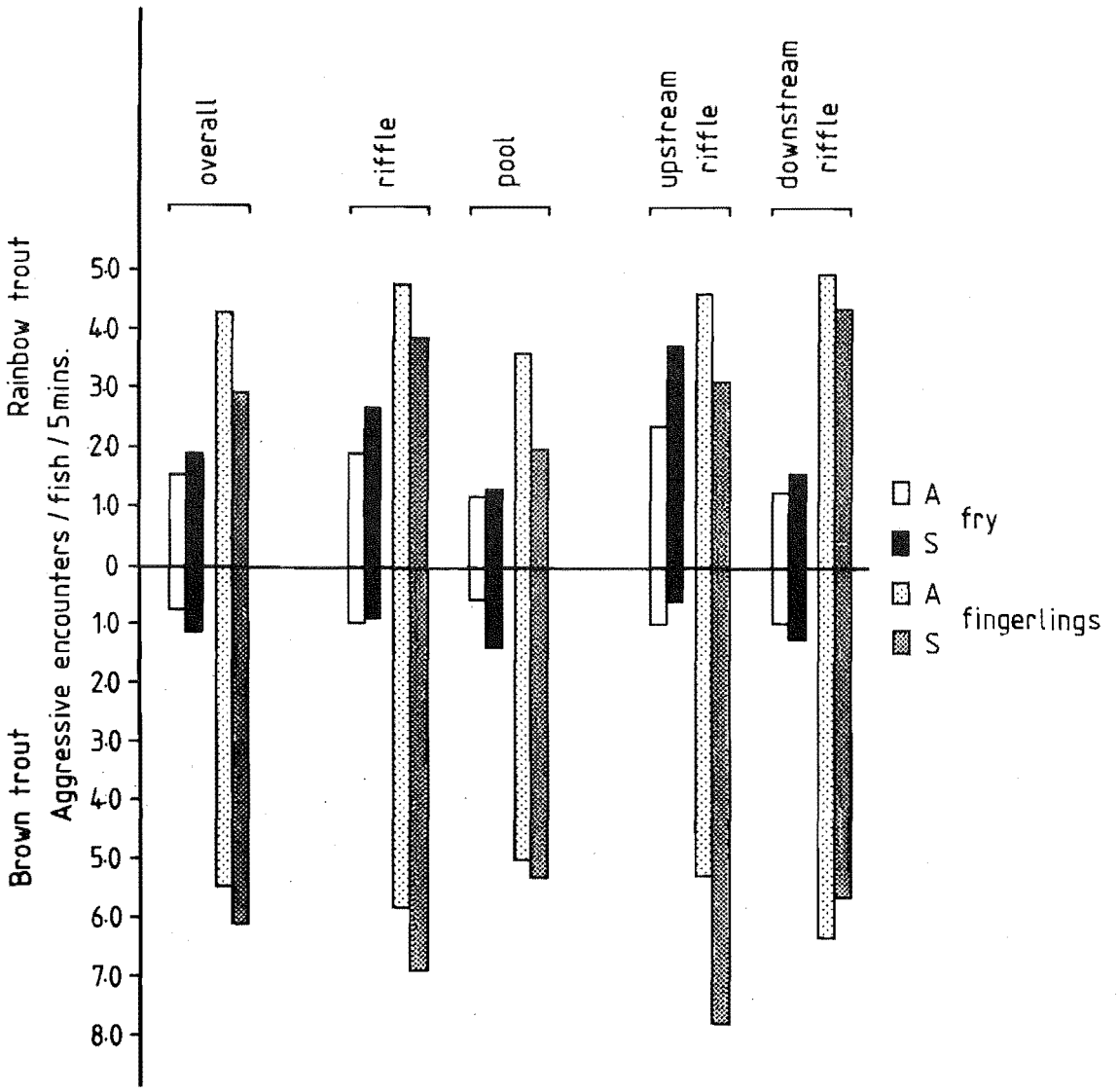


Figure 6.5 Comparisons of species rates of aggression in allopatry and in sympatry overall, and in each microhabitat, for brown and rainbow trout of the two size classes.

aggressiveness in the fry stage, and increasing aggressiveness of brown trout while decreasing aggressiveness of rainbow trout in the larger size class (Fig. 6.5). These changes in aggression were however, significant only for rainbow fingerlings (Table 6.11). In the upstream riffle, differences between the species were greater in sympatry than in allopatry in both size classes. This was also the case for fingerlings in the pool. Social dominance of rainbow fry in the upstream riffle was manifested in high levels of aggression by that species corresponding

Table 6.11 Comparison of mean species rates of aggression ± S.E. in allopatry with species rates of aggression in sympatry in each microhabitat (U test significance levels * = 0.05%, ** = 0.01%).

	Rainbow fry			Rainbow fingerlings			Brown fry			Brown fingerlings		
	allopatry	sympatry		allopatry	sympatry		allopatry	sympatry		allopatry	sympatry	
Pooled total all habitats	1.58 ± 0.252	1.94 ± 2.90	NS	4.35 ± 0.538	2.97 ± 0.386	**	0.72 ± 0.108	1.12 ± 0.265	NS	5.41 ± 0.566	6.06 ± 0.491	NS
Riffle	1.94 ± 0.304	2.71 ± 0.404	NS	4.85 ± 8.33	3.94 ± 0.518	NS	0.94 ± 0.143	0.86 ± 0.243	NS	5.79 ± 0.797	6.82 ± 0.813	NS
upstream riffle	2.41 ± 0.580	3.78 ± 0.682	NS	4.68 ± 0.442	3.18 ± 0.260	NS	0.95 ± 0.181	0.56 ± 0.171	NS	5.27 ± 1.092	7.71 ± 1.344	NS
downstream riffle	1.32 ± 0.245	1.64 ± 0.469	NS	5.03 ± 0.964	4.45 ± 0.813	NS	0.92 ± 0.185	1.18 ± 0.356	NS	6.30 ± 0.949	5.68 ± 0.755	NS
Pool	1.23 ± 0.381	1.34 ± 0.391	NS	3.69 ± 0.662	2.03 ± 0.553	*	0.52 ± 0.146	1.34 ± 0.462	*	4.94 ± 0.779	5.28 ± 0.557	NS

with low levels of aggression by brown trout, and explains the observed displacement of brown fry from this habitat in sympatry. I expected to see the opposite result in the lower riffle in accordance with the displacement of rainbow fry from this habitat in sympatry. Although such a result was not observed, an indication of the diminished competitive vigour of rainbow trout, both in the lower riffle and in the pool, was reflected in their low interspecific levels of aggression in these habitats (Fig. 6.6). This observation corresponds with higher interspecific levels of aggression in brown fry. As fingerlings, brown trout were most socially dominant in the upstream riffle, as revealed by the very high interspecific level of aggression in this species corresponding with the low level in rainbow trout (Fig. 6.6). This explains the observed displacement of rainbow fingerlings from the upstream riffle in sympatry.

Levels of intraspecific aggression in brown trout of both size classes were consistently lower than interspecific levels (Fig. 6.6), although not always significantly lower (Table 6.12). Brown trout were very sedentary and strongly territorial, and generally appeared to avoid territories of conspecifics. This behaviour served to minimize contact and hence aggression between brown trout. Such behaviour was not as common in rainbow trout.

The difference between intra- and interspecific rates of aggression of brown fry was greater in the pool than in the riffle and yet, unlike that in the riffle, was not statistically significant (Table 6.12). This non-significant result was caused by lack of homogeneity of variances in the pool data.

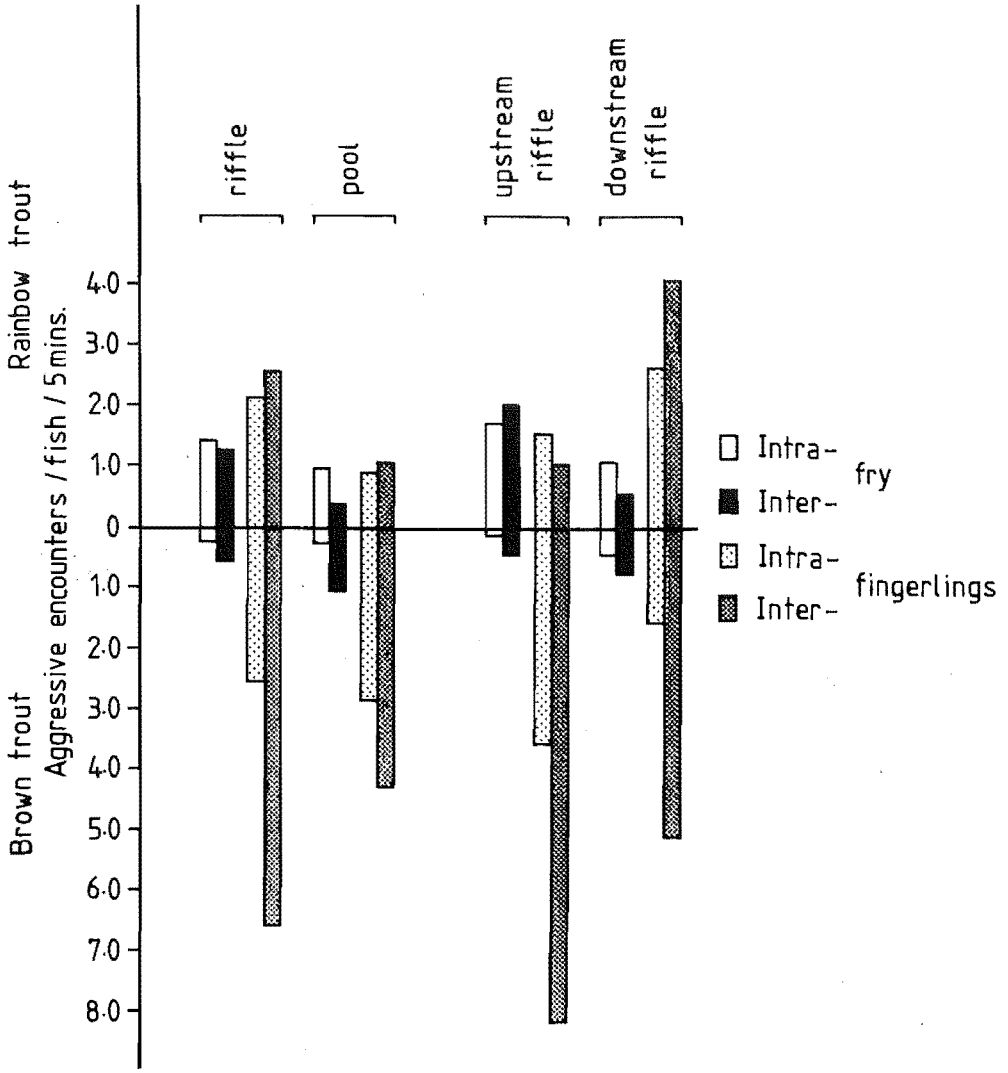


Figure 6.6 Comparison of intraspecific and interspecific rates of aggression in sympatry in each microhabitat for brown and rainbow trout of the two size classes.

Table 6.12 Comparison between intra- and interspecific mean rates of aggression ± S.E. in each microhabitat for both size classes of each species. (U test significance levels * = 0.05%, ** = 0.01%).

	R.fry			R.fing.			B.fry			B.fing.		
	intra-	inter-		intra-	inter-		intra-	inter-		intra-	inter-	
Riffle	1.41 ± 0.222	1.28 ± 0.326	NS	2.11 ± 0.438	2.58 ± 0.508	NS	0.28 ± 0.112	0.59 ± 0.142	*	2.57 ± 0.688	6.58 ± 0.982	**
upstream riffle	1.73 ± 0.338	2.01 ± 0.581	NS	1.57 ± 0.502	1.06 ± 0.292	NS	0.12 ± 0.050	0.41 ± 0.158	NS	3.55 ± 1.270	8.12 ± 1.529	*
downstream riffle	1.09 ± 0.382	0.55 ± 0.210	NS	2.65 ± 0.659	4.10 ± 1.079	NS	0.43 ± 0.238	0.75 ± 0.203	NS	1.58 ± 0.340	5.09 ± 1.170	**
Pool	0.96 ± 0.332	0.38 ± 0.121	NS	0.90 ± 0.245	1.09 ± 0.189	NS	0.28 ± 0.083	1.07 ± 0.471	NS	2.86 ± 0.492	4.27 ± 0.655	NS

6.3.3.3 PRIOR RESIDENCE

Prior residence by a species resulted in increased aggression in that species and reduced aggression in the intruding species in most microhabitats (Fig. 6.7). However, most of these changes in aggression were not statistically significant due to large variances in the data (Table 6.13). Increased aggression in species given prior residence arose largely through increased interspecific aggression, i.e., individuals became more aggressive toward intruders. This result accords with the finding by Braddock (1949) that prior residence increases the potential for dominance in an individual. Most of these interspecific aggressive encounters occurred, particularly initially, because the intruding fish did not recognize territorial boundaries already learnt by resident fish. Social dominance, as revealed in levels of interspecific aggression, of rainbow fry in the upstream riffle was increased with prior residence and decreased when brown fry had prior residence (Fig. 6.8). These levels of interspecific aggression were significantly different between the two prior residence experiments ($P < 0.05$, U test) but not between each prior residence experiment and the no prior residence sympatry experiment.

When either species had prior residence, interspecific levels of aggression in brown fry were always greater (although not significantly greater) than intraspecific levels of aggression (Fig. 6.8). However, the cause of these differences was not the same in the two situations. When rainbow fry had prior residence the higher interspecific than intraspecific aggression in brown fry could be attributed to a defensive response to aggression initiated by rainbows; whereas, when browns had prior residence the higher interspecific level of aggression could be attributed to higher levels of offensive aggressive activity directed toward rainbow fry. This difference was revealed in a significantly higher frequency of the defensive component of aggression (i.e., the

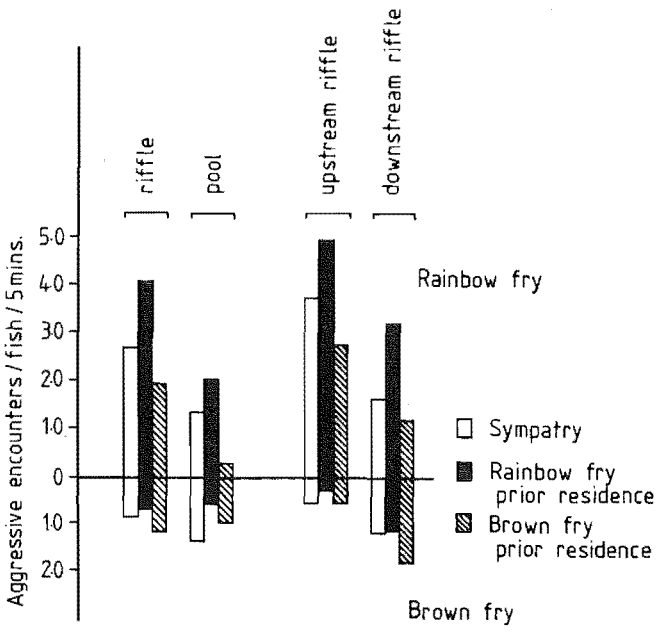


Figure 6.7 Comparison of mean species rates of aggression in sympatry and when either species was given prior residence in each microhabitat.

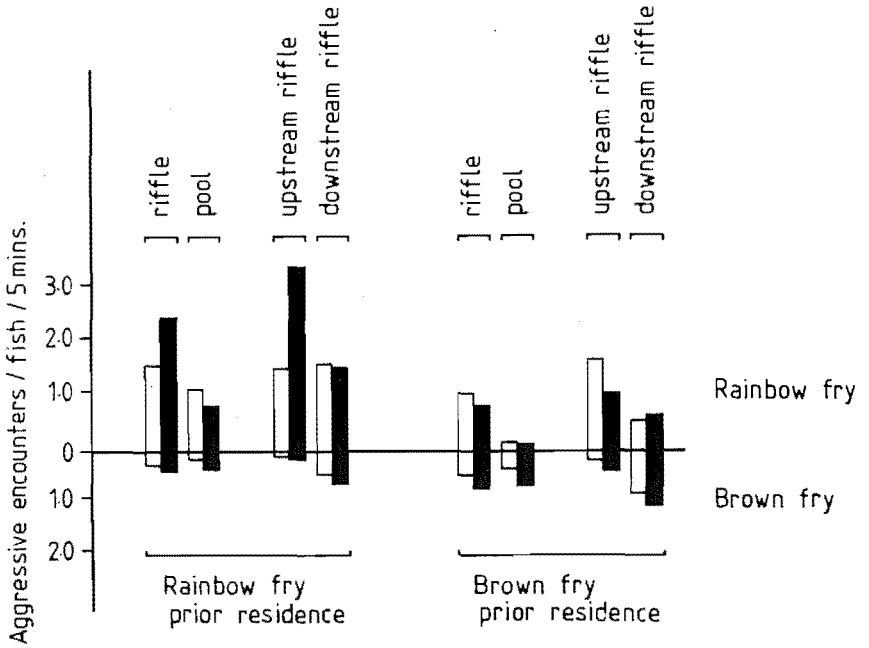


Figure 6.8 Comparison between intraspecific (clear bars) and interspecific (dark bars) rates of aggression for each species when either species was given prior residence.

Table 6.13 Comparison between mean species rates of aggression ± S.E. in sympatry and mean species rates of aggression when either species was given prior residence (U test significance level * = 0.05%).

	Sympatry		R.fry with prior residence				B.fry with prior residence			
	R.fry	B.fry	R.fry		B.fry		R.fry		B.fry	
Riffle	2.71 ± 0.404	0.86 ± 0.243	4.10 ± 0.717	NS	0.68 ± 0.197	NS	1.99 ± 0.398	NS	1.16 ± 0.202	NS
upstream riffle	3.78 ± 0.682	0.56 ± 0.171	4.98 ± 1.452	NS	0.29 ± 0.082	NS	2.78 ± 0.693	NS	0.55 ± 0.207	NS
downstream riffle	1.64 ± 0.469	1.18 ± 0.356	3.21 ± 0.583	*	1.12 ± 0.362	NS	1.21 ± 0.465	NS	1.80 ± 0.380	NS
Pool	1.34 ± 0.391	1.34 ± 0.462	2.04 ± 0.508	NS	0.54 ± 0.119	NS	0.30 ± 0.080	*	0.97 ± 0.195	NS

lateral display) ($P < 0.01$, Chi-square), and significantly lower frequencies of offensive components of aggression ($P < 0.01$) in such encounters when rainbows had prior residence, than when browns had prior residence.

Brown fry appeared to be unable to maintain the behavioural advantage (manifested in high levels of interspecific aggression) acquired through prior residence, particularly in the upstream riffle. When brown fry had prior residence they initially vigorously defended their territories against intruding rainbow fry. However, this behaviour quickly changed to one of submissiveness. This change in behaviour was reflected most clearly in the rapid reduction in aggression of brown fry with time, corresponding with a rapid rise in aggression of rainbow fry in the upstream riffle (Fig. 6.9). Changes in aggression with time were not statistically significant due to large variances in the data, arising

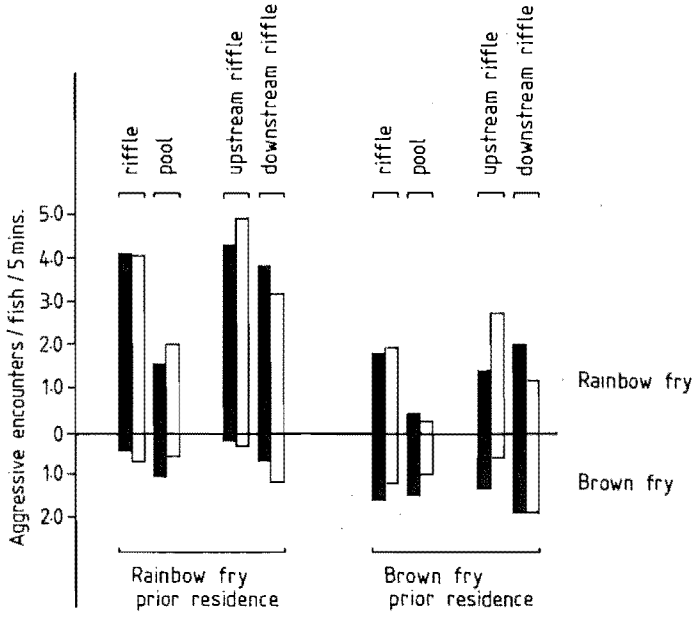


Figure 6.9 Comparison between mean species rates of aggression recorded in the first two days (dark bars) and during the remaining days (clear bars) of each experiment in each microhabitat when either species was given prior residence.

partly from the speed of the changes. It appeared that a similar, though lesser (also not significant), trend occurred in reverse in the downstream riffle when rainbow fry had prior residence (Fig. 6.9). However, in this case levels of aggression in brown fry did not exceed or even approach those of rainbow fry by the end of the experiment, implying that rainbows retained their behavioural advantage. Maintenance of high levels of interspecific aggression by rainbow fry in all microhabitats presumably was responsible for the high emigration rate of brown fry observed in this experiment (Fig. 6.2).

6.3.3.4 SIZE DEPENDENT AGGRESSION

Aggression between fish of the two size classes was minimal. In all microhabitats between-size-class aggression was much lower than within-size-class aggression (Fig. 6.10, Table 6.14). Maximum distance at which fingerlings responded aggressively toward intruders was also greater toward fish of similar size than toward fry. Results of the experiments involving both species as fingerlings and recently emerged rainbow fry in sympatry were similar to those above. On occasions rainbow fry appeared closer to the substrate in the presence of fingerlings of either species, than in their absence.

Table 6.14 Comparison between mean within-size-class and between-size-class rates of aggression ± S.E. of brown and rainbow fingerlings and rainbow fry in the mixed size class experiments (U test significance levels * = 0.05%, and ** = 0.01%).

	Rainbow fingerlings x rainbow fry						Brown fingerlings x rainbow fry					
	R.fing.			R.fry			B.fing.			R.fry		
	within-size-class	between-size-class		within-size-class	between-size-class		within-size-class	between-size-class		within-size-class	between-size-class	
Riffle	2.40 ± 0.650	0.39 ± 0.120	NS	2.99 ± 0.856	0.62 ± 0.146	**	4.28 ± 0.607	0.46 ± 0.058	**	1.85 ± 0.312	0.57 ± 0.056	**
upstream Riffle	3.27 ± 1.098	0.45 ± 0.228	NS	3.81 ± 1.709	0.43 ± 0.118	**	3.44 ± 0.873	0.46 ± 0.086	**	2.33 ± 0.304	0.50 ± 0.096	**
downstream Riffle	1.52 ± 0.618	0.36 ± 0.093	NS	2.18 ± 0.474	0.80 ± 0.303	**	5.11 ± 1.081	0.45 ± 0.092	**	1.36 ± 0.422	0.65 ± 0.125	NS
Pool	1.64 ± 1.024	0.48 ± 0.148	NS	1.22 ± 0.311	0.77 ± 0.293	NS	2.56 ± 0.368	0.53 ± 0.103	**	0.73 ± 0.227	0.18 ± 0.045	NS

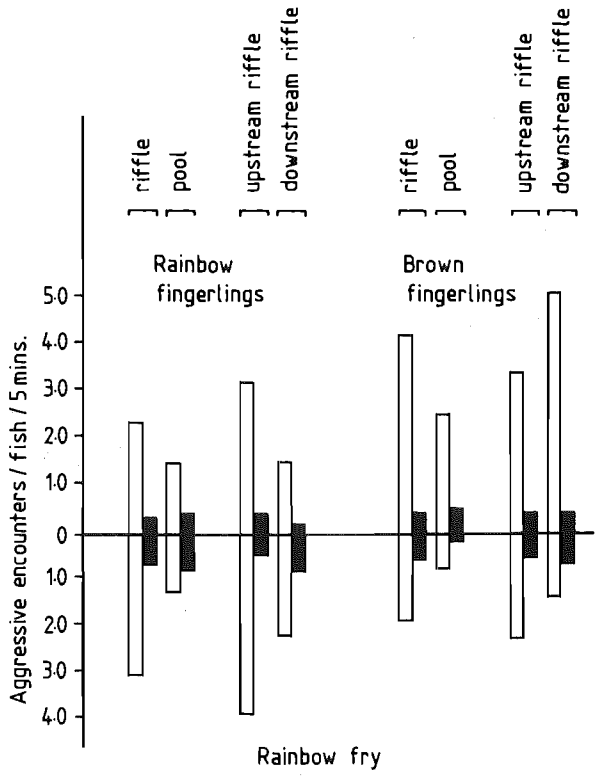


Figure 6.10 Comparison between mean within-size-class (clear bars) and between-size-class (dark bars) rates of aggression in fingerling brown and rainbow trout and rainbow fry in the mixed size class experiments.

6.4 DISCUSSION

6.4.1 GENERAL MICRODISTRIBUTIONS AND SOCIAL INTERACTIONS

Underyearling brown and rainbow trout are potential competitors for food and space. They exhibit similar agonistic behaviours and socially interact. In Scotts Creek, emergence periods of the two species overlap. This presents the possibility that competition for rearing space occurs between early emerging brown and rainbow trout, and between these fish and late emerging rainbow fry, the former being competitively advantaged by their larger size and prior residence.

As recently emerged fry both brown and rainbow trout preferred the riffle microhabitat in experimental observation troughs. Due to the small size of the troughs and limitation of inflow, the riffle (particularly the upstream half) did not represent typical riffle habitat in Scotts Creek. In particular, water velocities were much lower in the observation troughs than in the stream. The riffle microhabitat referred to in the present study is more analogous to shallow stream margins and gentle riffles. These are the areas in which recently emerged fry are usually encountered in streams (Kennedy 1982, and personal observation). Rainbow fry were more rigid in their preference for the riffle habitat, particularly the upstream riffle, than brown fry, most probably reflecting a preference for faster water velocities by this species. Fingerlings exhibited less habitat preference which probably was partly related to a shift from shallow to deeper water with increasing size and partly due to lack of a sufficient range of habitats (particularly of fast water velocity) available to fingerlings in the observation troughs. Such habitat shifts with increase in size have been reported for juvenile riverine salmonids by a number of authors (e.g., Chapman and Bjornn 1968, Lister and Genoe 1970, Symons and Heland 1978, Kennedy and Strange 1982). Preference for the surface of the pool by fingerlings, particularly brown trout, also may have been related to attraction to higher water velocities near the surface, or to a greater reliance on surface food due to inadequate aquatic invertebrate drift in the pool. Egglishaw (1967) found that juvenile Atlantic salmon and brown trout fed more at the water surface in pools than in runs.

In sympatry recently emerged brown and rainbow fry interactively segregated within the riffle, with the socially dominant rainbow trout occupying the upper riffle (characterized by higher water velocities and greater turbulence) and brown fry occupying the lower riffle. Such segregation might be specific to the observation troughs, simply

resulting from the social dominance of rainbow trout excluding brown trout from the best feeding areas, i.e., near the inflow, or it might reflect a segregation with respect to water velocity potentially occurring in the natural environment. I suggest that if interspecific competition causes interactive segregation between sympatric brown and rainbow fry, rainbow fry will occupy the faster velocity and more open shallow water habitat, and brown fry will occupy the quieter margins near riparian or instream cover. In the observation troughs, brown fry sought instream cover underneath stones, and usually were closely associated with the substrate, except at the surface of the pool where they kept in close proximity to either overhead cover or the trough walls. Distribution of brown fingerlings clearly was related to overhead cover. This attraction to cover apparently persists with age. Lewis (1967) showed that adult brown trout preferred pools with extensive cover, and that velocity was of less significance in the relationship between density of brown trout and environmental features. The reverse was true for rainbow trout, with velocity assuming much more importance than cover.

With increase in size both species increased their aggression, with brown trout exhibiting a greater increase and achieving social dominance over rainbow trout. A consequence of this reversal in social dominance was that brown fingerlings excluded rainbow fingerlings from the upstream riffle and therefore from the source of incoming invertebrate drift. It is possible that reversal in social dominance may have resulted simply from a behavioural anomaly in rainbow fingerlings induced by lack of suitable habitat for these fish in the troughs. Fast, deep water was shown by Lewis (1967) to be the environmental feature of highest significance to rainbow trout, but was not represented in the troughs. Denial of voluntary residence may have produced artificially high densities of fingerlings and may partly have contributed to higher

rates of aggression in fingerlings than in fry. However, if the observed results reflect a real reversal in social dominance in the natural environment, it is interesting to speculate on its cause. As fry, brown trout exhibited different strategies from rainbow trout for securing space in the troughs. In shallow water brown fry established territorial mosaics (described by Kalleberg 1958), and adhered to strict territorial behaviour. The sedentary behaviour of brown fry, close association with the substrate causing visual isolation of individuals, and mutual avoidance of conspecifics all served to minimize contact and hence aggression in that species. Social organization of rainbow fry was less rigid than that of brown fry. Rainbow fry commonly formed partial territories. In these an individual defends an area against all but those superior in rank to the defendant (Greenberg 1947). This behaviour leads to the formation of loose local dominance hierarchies. High rate of activity in the water column and a lower incidence of mutual avoidance behaviour maximized contact, and hence aggression, between rainbow fry.

Of the various forms of dominance behaviour, dominance hierarchies and territorial behaviour represent the two extremes of absolute and relative dominance respectively (Kaufmann 1983). Selection would favour avoidance of dominant individuals when the outcome is highly predictable (as it is with territorial animals), and interactions that occur when dominants and subordinates (e.g., territory holders and intruders) initially come into contact apparently suffice, for the most part, to establish the subsequent relationships that exist among these individuals. Social organization in young rainbow trout is very plastic and is influenced by fish density and water velocity. Cole (1976) reported that high water velocity encouraged station maintenance and territorial behaviour in rainbow fry, especially at low fish density. Increased crowding of these fish suppressed territorial behaviour, and dominance hierarchies formed. Fish in less turbulent water flow tended to

form dominance hierarchies, with higher levels of agonistic encounters at all densities. A high rate of aggression would be advantageous to an individual in establishing high social status in a hierarchy because the outcome of an aggressive encounter is not predictable (as it is with the strongly territorial brown trout), since not all members of a group of fish will be dominant. Aggression is highest between fish of similar size in a hierarchy (Symons 1968). Hence aggression was high between rainbow fry in the present study since they were all of similar size.

Gibson (1981) concluded that the behaviour of rainbow trout changes with size from a highly aggressive and territorial riffle dwelling juvenile, to a less aggressive and more pool dwelling larger fish. In the present study, underyearling rainbow trout did not reduce aggression with increase in size (from approximately 30mm to 55mm in length) but they did become subordinate to brown trout. Size range of fish in the present study was less than the 8.8 to 17.0cm range referred to by Gibson.

In the present study, the large increase in aggression of brown trout with increase in size (from approximately 30mm to 53mm in length) appeared to coincide with a change in the character of territoriality in that species. Territories of brown fingerlings appeared to be more irregular in distribution and their positioning seemed to be related more strongly to environmental features, such as cover and water velocity, than those of brown fry. In a territorial mosaic fish will not experience equal growth and survival opportunities, since food and cover are not uniformly distributed in a lotic environment (Kleenleyside 1979). Thus some individuals will grow faster than others and will establish themselves where food and shelter are most available. Initial positioning of a fish in a favourable location may involve a degree of chance rather than being solely related to the competitive ability of an individual to acquire space. Since initial territories within the mosaic are likely to

be transitory, it may be more advantageous to limit aggression thus conserving energy for growth. Upon an increase in size and consequent energy store, and with subsequently chosen territories being potentially more valuable to an individual, higher rate of aggression would not only be more affordable but also more important to maintain possession of valuable resources. Increase in aggression and subsequent strengthening of territoriality would fit brown trout for prolonged stream residence. The more plastic social organization of rainbow trout, and lower levels of aggression in larger fish, might enable that species to adapt to the lentic environment more easily than brown trout, and at any stage in their post-emergent development.

In the experiments, both species increased the proportion of display over non-display components of aggression with increase in size. This has also been reported in juvenile Atlantic salmon (Kalleberg 1958). Rainbow trout agonistic behaviour changed from predominantly nipping to predominantly display. Hartman (1963) reported that fish in display postures apparently had difficulty in holding position in fast currents. The behaviour shown by rainbow fry would better suit them to faster currents, such as those encountered in riffles, than brown fry. Newman (1956) suggested that the greater use of threat by brook trout and their lower nipping frequency, compared with rainbow trout, may indicate a more advanced social behaviour in which injurious fighting is replaced by stereotyped non-injurious threat ceremonies (Tinbergen 1953) having the same function. Also, threat behaviour is likely to be less energy demanding than direct fighting.

6.4.2 PRIOR RESIDENCE

Prior residence by a species resulted in increased aggression in that species and reduced aggression of the intruding species. These changes in aggression were not accompanied by significant changes in microdistribution. There was some evidence of a slight extension of brown fry distribution, when given prior residence, into the preferred habitat of rainbow fry (i.e., the upstream riffle). In addition, brown fry may have been displaced from the troughs by rainbow fry with prior residence. Evidence from some published studies suggests that prior residence has a marked positive effect on dominance. Noakes (1978) reviewed studies by Miller (1957) on cutthroat trout, Chapman (1962) on coho salmon, Mason et al.(1967) on brook trout and Mason (1969,1975) on coho salmon, that showed greatly increased movement and reduced survival of fish recently introduced into a stream with a resident population. Introduced individuals apparently were forced to move, feed much less, and consequently suffered much higher mortality rates than resident fish (Stringer and Hoar 1955, Newman 1956, Miller 1958, Saunders and Smith 1962, Mason and Chapman 1965, Chapman 1966, Backiel and LeCren 1967). Generally, it has been concluded that the mechanism bringing about these effects is dominance of the resident fish over the introduced fish.

My results indicate that rainbow fry, but not brown fry, were able to maintain an advantage acquired through prior residence. Prior residence only advantaged brown fry in initial contacts with intruding rainbow fry. Chapman (1962) found that prior residence appeared to govern social position in hierarchies of coho salmon fry initially, but after a day size became more important. The situation in the present study agreed with that described for Platypoecilus maculatus, where prior residence only delayed the eventual victory of otherwise superior fish (Braddock 1945). The effect of prior residence in determining dominance

relationships can therefore gradually diminish with time, and other factors may predominate as the intruder becomes more familiar with the area (Braddock 1949). This situation applies with regard to higher potential for aggression as shown in the present study in which rainbow fry had a higher potential for aggression than brown fry, and also with regard to size, since larger individuals are more frequently dominant as time passes (Braddock 1949). Gibson (1981) also concluded that species and size, rather than prior residence, was of overriding importance in competitive interactions between juveniles of various species of salmonidae.

6.4.3 SIZE RELATED AGGRESSION

There are two seemingly contradictory concepts regarding the role of size in determining competitive interactions between animals (Wilson 1975); 1/ the concept that differences in body size set up a competitive gradient whereby the larger can exclude the smaller and 2/ the concept that differences in body size promote a "niche difference". In freshwater fish, whichever of these concepts prevails presumably depends upon the magnitude of the size separation. As riverine salmonids grow they move from quiet stream margins to faster deeper water. This results in spatial segregation of different size classes, and of potentially competitive species if emergence times differ (Everest and Chapman 1972). If similarity in size results in fish occupying the same microhabitat, there is potential for competition to occur. However, even then any size differences play an important role in determining levels of aggression and related dominant:subordinate roles. Greatest social conflict occurs between fish of similar size (Newman 1956 and Symons 1968). Slight differences in length (e.g., 1mm) of individual coho salmon

in contact pairs (pairs of fish interacting aggressively) were sufficient to bring about subordination of smaller fish (Chapman 1962). In the present study, lack of sufficient range of habitat in the observation troughs forced fingerlings and fry together whereas in the stream these fish are likely to be spatially segregated. However, my results show that even when fry and fingerlings occur in the same habitat aggression between these fish is minimal and interactive microhabitat segregation does not occur. Since differently sized fish are likely to require different food, behaviour which focuses competition for space on fish of similar size would be adaptive (Symons 1968). Thus there are two separate factors operating to reduce competition between fingerlings and fry; voluntary spatial segregation, and agonistic behaviour which focuses competition for space on fish of similar size.

Interactions that did occur between fingerlings and fry usually consisted of the dominant fingerlings chasing and nipping the fry. Some of these attacks may have resulted from an intention to eat, rather than drive away, intruding fry. Predation of brown fingerlings on rainbow fry was observed in the troughs. Fry may avoid aggression and predation by fingerlings by maintaining station close to the substrate and hiding amongst rocks when in the presence of larger fish; a behaviour observed in the present study and by Symons and Heland (1978) in juvenile Atlantic salmon.

In between-size-class interactions frontal display was suppressed by fingerlings. In classical ethological theory threat displays are considered to result from a conflict between tendencies towards attack and escape (Manning 1979). In the present study, recently emerged fry would not be expected to intimidate the much larger fingerlings; thus strong conflict between attack and escape should not occur in fingerlings during between-size-class interactions. Hence, in these interactions frequency of frontal threat display was reduced

whereas that of chasing increased.

In conclusion, my results show that underyearling brown and rainbow trout will compete for space in streams, the latter being socially dominant as fry in riffles and the former socially dominant in most microhabitats after the fry stage. This change in social dominance with increase in size may be related to differences between the species in the strategies that they employ for securing space within the stream environment. At the fry stage sympatric brown and rainbow trout apparently will partition space within the shallow stream habitat, with rainbow trout utilizing microhabitats with faster more turbulent water. Prior residence was not of great significance in determining dominance relationships and would be of minor importance in competitive interactions between early and late emerging underyearlings in Scotts Creek. On the other hand, size differences do play an important role in competitive interactions, but by minimizing competition between early and late emerging fish, rather than competitively advantaging the former.

CHAPTER VII

GENERAL DISCUSSION

7.1 COMPETITION BETWEEN BROWN AND RAINBOW TROUT IN THE CONTEXT OF COMPETITION AND NICHE THEORIES

Since Grinnell (1908) first combined the idea of competitive exclusion with the concept of the ecological niche, competition theory has been associated closely with niche theory. Competition should be understood in connection with the niche concept since some similarity or overlap in niches is a prerequisite of competition (Diamond 1978). Consequently I consider it appropriate initially to discuss the main findings of the present study within the context of niche theory and in doing so aim to reveal an inadequacy in the current presentation of Hutchinson's concept of the ecological niche. Hutchinson (1957) defined a niche as a region of multidimensional niche space (hypervolume), occupied by a species (or organismic unit, defined by Pianka (1981) as an organism or population of organisms) the axes of which represent all the possible environmental variables (or resources). When the niche is defined primarily without reference to competitors, but merely in terms of requirements and tolerances, it is referred to as the "fundamental" or "pre-interactive" niche. A species' exploitation of its entire fundamental niche is usually curtailed to various extents by competitors (and predators) and the resulting subset of niche space actually utilized is referred to as the "realized" or "post-interactive" niche. This is now the generally accepted concept of the ecological niche and as such is included in most recent ecology texts (e.g., Odum 1971, Hutchinson 1978, Krebs 1978 and May 1981).

The impression that most presentations of this concept impart is

that the niche is static temporally; and that competition for, and realized exploitation of, any one resource by a species is independent of competition for, and realized exploitation of, other resources characterizing the niche. Hutchinson (1957) recognized that his definition only described the niche at one point in time, but accepted it in this form for the sake of simplicity. However, simplistic presentations fail to depict the niche in terms of the complete life cycle of a species. Resource utilization commonly varies with time and the importance of any resource (or environmental variable) in determining species abundance, or competing species population equilibria, can depend on the age or particular developmental stage of the organism. This is most apparent in organisms such as fish, reptiles and many invertebrates which undergo successive stages in their life cycles where each stage is subject to population regulatory forces. Competition might potentially occur at any stage of such a life cycle and act to constrict the realized niche. However, the variables that constrain the realized niche of a species within its fundamental niche need not, as defined originally by Hutchinson (1957) and Vandermeer (1972), be limited to competitive interaction (Connell 1975). Other factors such as harsh physical conditions, parasitism, predation, density independent resource shortages and disease can reduce fecundity, fertility and longevity, so effectively limiting population numbers that potential competition is mitigated or precluded (Alley 1982). There is substantial evidence of the effectiveness of these and other density-independent factors in limiting populations (e.g., Connell 1975, Giesel 1974, Harrison 1964, Hutchinson 1978, Miller 1967, White 1978). In the context of multistage life cycles the potential for competition (and other density dependent population regulating factors) in a particular resource dimension, may be influenced by population regulating factors, including competition in other resource dimensions, acting during previous stages in the life cycle.

Competition occurring at various stages in the life cycle may involve the same or different species. Competition between the same competitors at successive stages in their life cycles would be most likely to occur between taxonomically closely related species. Brown and rainbow trout are examples of such species. Being closely related, and having very similar life cycles and ecological requirements and habits, they potentially compete at all stages of their life cycles i.e., during the reproductive, juvenile and adult stages. During each stage the critical resources which are utilized, and which have the potential to shape the realized niche of each species,are different. The results of the present investigation into competition between these two species in the first two stages of their life cycles demonstrate the temporal complexity of competition and the niche referred to above. In Scotts Creek, interference competition for spawning space, both intra- and interspecific, mediated through redd superimposition, is the major factor determining absolute and comparative species abundance of juvenile brown and rainbow trout, and the temporal pattern of rainbow trout fry emergence. Thus it predetermines the realization of the potential for subsequent intra- and interspecific competition, and resultant resource sharing, between juveniles in Scotts Creek and possibly between juveniles and between adults in Lake Alexandrina.

Given the wide scope for competition (and other population regulating factors) to act throughout the life cycles of these species, and the complex interdependence between potentially critical resources, it is not surprising that there is a large degree of variation in population equilibria of sympatric populations of these two species in different systems. Conventional simplistic presentations of competition and niche theory, while useful in providing a conceptual framework for basic understanding of the niche concept and resource sharing, fail to model the complex niche interactions amongst species assemblages in the

context of population regulatory forces acting over the lifetimes of those species. Such complex interactions appear to be the rule rather than the exception in nature, particularly in fish communities.

The conventional simplistic approach to competition and niche theory has been questioned by some theoretical ecologists in recent years (e.g., Giesel 1974, Wiens 1977, Wangersky 1978, den Boer 1980, Alley 1982). The viewpoint of such authors is similar to that expressed by Neill (1974, p.399): "The nearly complete dependence of theoretical community ecology on a limited number of simple models (such as the Lotka-Volterra competition equations) has resulted in the development of subsequent generations of deceptively simple constructs that may often confuse our understanding of the underlying biology rather than improve it". A viable definition of the niche needs to be based more on ecological data from natural communities, and less on idealized ecological models and data from highly artificial laboratory experiments (Alley 1982). As a contribution to this new approach to competition and niche theory, I propose that Hutchinson's framework of the niche concept should be extended to present the niche as a potentially temporally dynamic hypervolume occupied by an organismic unit during its lifetime. The potentially critical resources (subset of all the possible environmental or resources) which determine the realized niche at any point in time may vary with the different stages in the organismic units' life cycle. These temporal changes in potentially critical resources promote an interdependence between those resources; since the extent of realized exploitation of some resources may be determined by population regulatory mechanisms acting previously on other critical resources. Competition should be viewed as one of a number of population regulatory mechanisms determining realized exploitation of resources. The importance of interspecific competition in shaping the realized niche will depend on comparative species abundance and related resource supply in shared

resource dimensions.

The ubiquitous role of competition in nature has been questioned by some authors (e.g., Birch and Ehrlich 1967, Paine 1971, Culver 1975, Connor and Simberloff 1979, and see review by Schoener 1982). This scepticism arises partly from the overemphasis imparted to competition by conventional competition theory and also from the scarcity, until recently, of direct documentation of competition in nature. While interspecific competition should not be viewed as ubiquitous in nature, its existence and effectiveness as one mechanism regulating species abundance and exploitation of resources must not be underestimated, as my study clearly shows.

7.2 INTERFERENCE COMPETITION FOR SPAWNING SPACE

Interference is the most direct and most apparent form of competition, and is therefore easier to demonstrate than exploitation competition. In the present study interference competition, acting at the reproductive stage of the life history, was the major factor determining comparative species abundance of brown and rainbow trout. "In general, interference by individuals in a population will cost them something in terms of rate of resource exploitation and therefore rate of population growth, since they will have to spend some time and energy in acts of interference which consume time and energy that would otherwise be devoted to resource exploitation" (Case and Gilpin 1974). While this generalization is true for most forms of interference competition (including aggression- mediated competition for space between juvenile salmonids) it does not hold for interference competition for spawning space (mediated through redd superimposition). Such competition is "gratuitous", and acts indiscriminantly of species as a result of normal

spawning activities. Acts of interference by an organism usually deny a competitor access to resources. However, in the case of interference competition for spawning space (mediated through redd superimposition) initial access to resources is generally unrestricted (except when numbers of concurrent spawners temporarily exceed available space) but their continued use is denied. The embryos need for their development not only space within the gravel, but also an adequate circulation of water to remove waste metabolites and to supply oxygen. Since gaining access to these resources commits the progeny to their continued use, subsequent denial of their use, caused directly by displacement from the gravel or indirectly by alteration of the water supply, is lethal, as is direct physical injury caused by the interference. The lack of parental care, and the long period of development in the gravel, leaves embryos particularly vulnerable to such interference.

Interference competition for spawning space acts similarly to predation of eggs or immature forms of a resource competitor. The cost of both forms of interference is very low (even negative in the case of predation) but the effect on directly limiting the abundance of a competitor is great. Interference egg predation was a major factor causing the elimination of species of granivorous insects in studies of interspecific competition by Park (1948, 1954,1962) and Crombie (1944,1945). Environmental harshness or variability can also act at the egg or larval stage and produce the same effects as interference competition. For example, Segrist and Gard (1972) reported that species dominance in sympatric populations of brook and rainbow trout in Saghen Creek, California, was dependent on timing of floods. Winter floods decimated the developing eggs of fall-spawning brook trout which enhanced the survival of later emerging rainbow trout through reduced interspecific competition at the fry stage. Conversely, spring floods destroyed rainbow eggs, thereby enhancing the survival of brook fry. This

example is pertinent to the present study since it represents another situation in which a population regulatory force acting at one stage in sympatric species' life cycles effects interspecific competition at a later stage.

Most studies of competition in freshwater fish have been concerned with competition for food or space (food related) between juveniles or adults. However, most of the evidence for competition for these resources is largely inferential, and direct quantitative evidence of competition between freshwater fish (in the form of lowered species abundance) is rare. This situation can be attributed largely to the generalist habits of freshwater fish which are adapted to a changeable environment. Larkin (1956) concluded that "freshwater environments are characterized by the lack of opportunity they offer for specialization of animals. This feature is reflected in the versatility and plasticity of fishes, and the consequent vagueness and complexity of interrelationships between fish species...". Frequent outcomes of living in unpredictable environments are large niches and a high level of plasticity (Levins 1968). In freshwater fish communities, it is also difficult to separate the role of interspecific competition from other phenomena (e.g., predation and environmental influences) as a factor in population control, partly because of the interdependence between these variables and partly because they produce similar effects. Generalized feeding and habitat requirements allow freshwater fish to modify food and space utilization in response to interspecific competition for these resources, thereby minimizing its severity (and therefore its detectability). In contrast to generalization in food and habitat dimensions, freshwater fish exhibit much greater specialization in breeding habits. Within the Salmonidae, requirements for spawning site are restrictive and similar. Thus, as Larkin (1956) predicted, although competition for spawning site probably occurs less frequently than competition for food (or food

related space), when it does occur it is likely to be more severe and its effects considerably more damaging to a population, as my results demonstrate.

In addition to the obvious direct effects which competition for spawning space has on comparative species abundance, it is interesting to consider the more subtle effects this competition may have on timing of the spawning runs in Scotts Creek. If it is assumed that trout produced in Scotts Creek home back to the stream to spawn and that the time of their return is genetically controlled, then interference competition for spawning space would select for late returning fish. Homing of salmonids, well known amongst anadromous forms (Taft and Shapovalov 1938, Scheer 1939, Foerster 1968), also has been demonstrated for non-anadromous forms in other lakes. Vernon (1957) showed that kokanee homed to inlet streams in three areas of Kootenay Lake, with less than three percent straying. Stuart (1957) showed that brown trout also homed strongly to specific inlet spawning streams entering a Scottish reservoir. Lindsey et al. (1959) demonstrated that homing of rainbow trout into inlet and outlet streams of a British Columbia lake was 94% effective. Observations have been made of quite specific temporal consistency in upstream migration of repeat spawning rainbow trout in a spawning tributary of Lake Rotorua, New Zealand (P. Mylechreest pers. comm.). Evidence for selection for late spawning fish in Scotts Creek is seen in the positively skewed temporal distribution exhibited by the rainbow trout spawning runs. Selection favours rainbow trout over brown trout because the spawning season of the former is more extended and continues later than that of brown trout. At present, the extended spawning season of rainbow trout, which completely overlaps the spawning season of brown trout and the entire incubation period of the brown trout embryos, ensures that selection does not proceed in the reverse direction producing temporal separation of the spawning runs. However, if genetic control of timing is reasonably

specific and if selection for even later spawning in rainbow trout continues, it is possible that numbers of fish returning during the middle of the rainbow trout spawning period (i.e., during late June to early August) will decline enabling the progeny of very early spawners (including both brown and rainbow trout) to survive. This could result in selection for very late and very early spawners and produce a bimodal run of rainbow trout, of which the early peak would be accompanied by a run of brown trout. However, selection in either direction ultimately would be limited by environmental factors, (e.g., temperature and related food availability) which may act against survival of embryos and fry. Thus the temporal pattern of spawning can be envisaged as being in equilibrium between internal competitive forces acting outwards and external environmental, and possibly biological, forces acting inwards.

In conjunction with external factors limiting the extent of selection for late spawners, selection also may be moderated by competitive effects which negate the influence of tight genetic control of timing of return of late spawners in driving selection. If, as has been suggested in Section 4.7.4, spatial constraints of the spawning ground cause an accumulation of late spawning rainbow trout in the stream, timing of spawning will be largely independent of time of arrival since fish which have arrived at various times will all be competing for a limited number of spawning sites. Bearing in mind that only the latest spawning fish have any real spawning success, such a mechanism would introduce an element of chance into the relationship between timing of arrival and spawning success, thus weakening the selection pressure for late arrivals. Thus it is perhaps easier to envisage selection acting broadly on time of spawning through maturation of gametes, than acting more precisely on time of return to the spawning ground.

7.3 COMPETITION BETWEEN UNDERYEARLINGS IN RELATION TO MIGRATORY STRATEGIES

Now I would like to consider the significance of potential and realized interspecific competition between underyearlings in Scotts Creek in regulating populations of brown and rainbow trout in Lake Alexandrina.

In the small stream environment the niches of underyearling brown and rainbow trout broadly overlapped and my experimental evidence showed that they will compete for space. Mutual agonistic interference appeared to be the main mechanism by which the fish competed both intra- and interspecifically. Interspecific agonistic behaviour was similar to intraspecific behaviour and I consider it occurs as a result of mistaken identity due to similarities in body size, colour patterns and behaviour between the species. This idea was proposed by Murray (1971) and Grant (1972) as a possible explanation for interspecific agonistic behaviour in birds and rodents respectively. A population that interferes intraspecifically may be highly preadapted for interspecific interference (Case and Gilpin 1974). It is inferred from my experimental evidence that interspecific agonistic interference in large part induced microhabitat segregation between brown and rainbow trout fry within the shallow gentle riffle:run habitat preferred by fry. Under intense interspecific competition, sympatric populations of closely related species narrow their range of resource utilization and compete under those conditions to which each is best adapted, or where each has some competitive advantage (Nilsson 1956). In sympatry, brown fry reduced utilization of the faster, turbulent, and possibly more open, gentle riffles, the preferred microhabitat of rainbow fry, whereas rainbow fry reduced utilization of the slower shallow runs. In the fast-water habitats rainbow fry were socially dominant and appeared to be effective interference competitors against brown fry. Conversely, although not as clearly socially dominant,

brown fry appeared to effectively interfere with rainbow fry in the slow-water habitats. Hydromechanically the predominant agonistic behaviours of rainbow trout (i.e., nipping and chasing) are more suited to faster velocity habitats, whereas those of brown trout (i.e., threat displays) are more suited to slower velocity habitats. In addition, interactive segregation of the type observed between brown and rainbow fry may be maintained by differences in motivational states of the species in different microhabitats, with motivation to defend resources being highest in the preferred or optimum microhabitat (Hartman 1965). Rainbow fry were more inclined to defend the faster velocity habitats, as evidenced by their higher rates of aggression in such habitats, and to a lesser extent brown fry were more inclined to defend the slower velocity habitats, as evidenced by higher interspecific rates of aggression in such habitats.

The experimental evidence suggests that the dominance relationship between underyearling brown and rainbow trout is dependent on stage of development. As fry, rainbow trout were socially dominant over brown trout, at least in fast-water habitats, whereas as fingerlings, brown trout were clearly socially dominant in all microhabitats tested. If this change in dominance with age is a real phenomenon, and not simply an artifact of the experimental environment, then it is worthy of closer investigation. Available evidence suggests that consideration of differences in social structure and in related strategies of space acquisition between the species might prove a fruitful approach to such an investigation. Putting the influence of modifying factors aside (e.g., size differences and imbalance in species composition), my results indicate that in the stream environment, brown trout, once past the fry stage, socially dominate rainbow trout and probably exclude rainbow trout from the best feeding areas in slow-water habitats (i.e., runs and pools) and possibly in much of the riffle

habitat. Possibly open, fast, deep-water habitat would provide refugia for rainbow trout faced with competition from brown trout.

The potential for interspecific competition between underyearlings to regulate populations of sympatric brown and rainbow trout depends on its severity, but also in lake tributary systems, such as the one under investigation, it will depend upon the importance to each species of the spawning tributary as a primary feeding area. Thus, interspecific competition between underyearlings should be discussed in the wider context of the migratory strategies employed by each species in relation to stream versus lake rearing.

With many species which undergo a period of residence in the parental spawning habitat, survival apparently is enhanced by attaining a certain size before migrating to the secondary feeding habitat, such as a lake (Northcote 1967). A pertinent example of this situation, and one which is directly comparable with the present study, is given by Tilzey (1972) of sympatric underyearling brown and rainbow trout in inlet spawning tributaries of Lake Eucumbene, Australia. In that system the majority of rainbow trout migrated soon after emergence, apparently in response to interspecific competition with earlier emerging brown trout, and incurred heavy mortality through predation upon entry to the lake. Much of this predation was attributed to adult brown trout that congregated at the lotic:lentic interface. In contrast, brown trout remained in the natal streams for at least a year before migrating, and apparently their larger size upon entry into the lake contributed to their lower mortality and numerical dominance over rainbow trout.

On the other hand, by migrating from the spawning stream shortly after emergence fry may avoid some of the heavy mortality often associated with the establishment of territory by juveniles resident in streams. Observations of Benson (1960) on cutthroat trout entering Yellowstone Lake, Wyoming suggested that output of juvenile cutthroat

trout from tributary streams to the lake may have been heavily dependent on fry which moved downstream shortly after emergence, rather than on those which remained in the spawning streams over the winter and longer. Abundance of food in lakes may favour survival and growth of early migrants (Benson 1960). Mottley (1932) demonstrated that young rainbow trout which migrated from an inlet stream to Paul Lake, British Columbia shortly after emergence showed an appreciable increase in growth rate over those that remained several weeks or months longer in the inlet stream. The latter may eventually attain a size comparable to the lake type fish but may take several years to do so. Potentially faster growth in the lentic environment may increase survival of early migrants indirectly by shortening the period in which they are vulnerable to predators. LeCren (1962) observed that young trout migrating to Three Dubs Tarn as alevins had a higher mortality as well as an increased growth rate compared with those few which entered the tarn somewhat later. These later migrating fish had a higher survival but a slower growth rate while in the inlet stream. Thus early migrants may experience lower survival initially than those which remain in the nursery stream, but this may be compensated for by faster growth and related higher survival and possibly higher fecundity later in life. The relative contributions that each group makes to adult recruitment is therefore complicated by the interplay between numbers, mortality, growth rate and timing of migration.

In the Lake Alexandrina system, the most advantageous migratory strategy for maximizing survival might be different for each species and may be determined by differences in behaviour. Underyearling brown trout appear to be adapted more rigidly to the lotic environment, as evidenced by their social behaviour, length of stream residence (which is related to "dispersiveness" on emergence) and lack of variability in behaviour patterns. Thus a period of stream residence might be mandatory to

maximize survival in this species. In contrast underyearling rainbow trout exhibit a plasticity in social behaviour which may allow them to adapt more readily, at any stage in their life cycle, to lentic conditions. Greater plasticity in behaviour is expressed in greater variability in timing of migration. Just as Benson (1960) observed in cutthroat trout, rainbow trout fry output from Scotts Creek is heavily dependent on early migrants. There appears to be no reason to suspect high mortality of early migrants entering Lake Alexandrina (T.G. Northcote pers. comm.); there is abundant riparian and aquatic vegetation cover for fry close to the lakes' shore, particularly in the vicinity of Scotts Creek, and there are no congregations of predators near the creek mouth when large numbers of fry migrate to the lake. Available evidence suggests that predation on fry by adult trout, perhaps the greatest predation threat, is insignificant at least within the stream. Early migrant rainbow fry must experience reasonably high survival since the low output of stream reared juveniles (only 8157 in total in 1980-1981, including many with very short residence times) cannot account for the large number of adult returns (assuming homing occurs). Thus early migrants would seem to contribute significantly to returns of rainbow trout.

Downstream migration of early migrants does not appear to be in response to either inter- or intraspecific competition, but rather it seems to be a dispersal process characteristic of the developmental stage of fry. Dispersal of such fry into the lake may be simply fortuitous arising from the short length of the spawning stream or, particularly in rainbow trout, it may be a result of selection for high "dispersiveness" if stream residence is disadvantageous for survival. For example, high "dispersiveness" in emergent rainbow fry might be selected for to avoid increasing mortality experienced by stream residents over the summer, possibly caused by habitat limitations particularly for larger juveniles.

Timing of emergence and subsequent downstream dispersal of early migrants to the lake may be crucial in optimizing feeding conditions and survival. In this regard, redd superimposition has the insidious effect of modifying the timing of migration by delaying peak emergence. Thus a population might arrive at a state where its survival potential is greatly impaired because of lateness of egg deposition (McNeil 1964). Whether delay of fry migration caused by redd superimposition does, or does not, affect the survival potential of rainbow trout from Scotts Creek is open to speculation. At least as far as the availability of planktic food items is concerned, precise timing of emergence and subsequent migration would not appear to be of importance. Daphnia carinata, potentially one of the most important planktic food organisms for trout fry in Lake Alexandrina, usually has been abundant during spring and early summer and exhibited no pronounced peak period of abundance during this time (V.M. Stout pers. comm.). The continued occurrence of a late spawning peak in the rainbow trout run would appear to imply that delay of peak fry migration is not very damaging to the survival potential of rainbow trout. The most significant effect of late emergence might be simply to reduce the growth potential of fry through shortening of the first summer growing period.

Thus it appears that if severe interspecific competition between underyearlings occurred, possibly eventually resulting in displacement of rainbow trout from the spawning stream, it would not necessarily significantly effect the population equilibrium of brown and rainbow trout in Lake Alexandrina since stream residence does not appear to be essential for maximizing survival of rainbow trout. However, in the present study the density of underyearling brown trout in Scotts Creek was too low for severe interspecific competition to occur. Hence, underyearling rainbow trout are able to coexist with brown trout in the spawning stream and extensively exploit this environment.

Understanding of competitive interactions and of niche partitioning between underyearling brown and rainbow trout in streams in New Zealand, where the species occur in unnatural sympatry, might be facilitated by considering the realized niche each species occupies in its native range in sympatry with its natural salmonid competitors. The native range of brown trout has its centre in Europe and the New Zealand stock originated in Great Britain, arriving via Tasmania (MacCrimmon and Marshall 1968). Brown trout occur in natural sympatry with Atlantic salmon in many waters in Britain and compete with this species at the juvenile stage (see for example Kalleberg 1958, Kennedy and Strange 1982, Kennedy 1982, Egglishaw and Shackley 1982). Rainbow trout are native to the west coast of North America (MacCrimmon 1971) and the New Zealand stock apparently originated from steelhead stock (anadromous rainbow trout) in Sanoma Creek, California (Scott and Fraser 1978). Glova (1978), commenting on the results of Hartman (1965), concluded that underyearling steelhead are social subordinates to coho salmon in coastal British Columbia streams. The range of coho salmon extends into California and includes the catchment from which the New Zealand stock of rainbow trout originated (Hart 1973). Steelhead are able to occupy a greater range of habitats than coho, but when in sympatry with coho are restricted to riffles and other fast-water habitats, where they have a competitive advantage. Conversely brown trout appear to be social dominants in their native range, occupying pools and other slow-water habitats. For example, Kalleberg (1958) concluded that brown trout parr were socially dominant over Atlantic salmon. Atlantic salmon apparently are somewhat analogous to steelhead in that they are predominantly riffle-dwelling social subordinates in streams (Kleenleyside 1962, Gibson 1966). Thus underyearling brown and rainbow trout are adapted to complementary niches and social roles in analogous geographically isolated communities, and they assume these same niches and social roles in unnatural sympatry in

New Zealand streams.

Social subordinates should show more plasticity (tendency to change behaviour as conditions change) than dominants (Morse 1974). Observations of the comparative behaviours of underyearling brown and rainbow trout in the present study support this view. The greater plasticity of rainbow trout gives that species greater scope to avoid interspecific competition by adjusting resource utilization particularly in lake tributary systems.

Populations that are dominant by virtue of interference competition are likely to suffer little niche contraction in the presence of competitors (Case and Gilpin 1974). However, when dominants are much rarer than subordinates (as in the present situation in Scotts Creek) the cost of excluding subordinates from marginal areas of the niche may become unprofitable. Therefore it may be advantageous for the dominants to retire from the least defensible parts of their fundamental niche (Morse 1974). Case and Gilpin (1974) demonstrated mathematically that the profit of interference by a population declines precipitously at high densities of a competing population. The maximum profits from interference occur at intermediate densities of competitors. It is highly unlikely that interference competition will operate to the total exclusion of exploitation competition (Miller 1967,1969). The socially subordinate species may exploit the dominants' resources to some degree even if the dominant restricts these opportunities. Exploitation competition would be particularly important when the subordinate species is present in much greater densities than the dominant (Morse 1974). Thus, in Scotts Creek, not only does the low abundance of underyearling brown trout free resources for the underyearling rainbow trout population, but the latter may obtain a greater share of the brown trouts' resources, as a result of niche contraction by that species and increased importance of exploitation competition, than it would if the

populations were more equal in size.

The above conclusion is most applicable to interspecific competition between underyearling brown trout and early emerging rainbow trout, although I suspect that competition between these fish is insignificant since densities are so low that resources are probably not in short supply. Interspecific competition between underyearling brown trout and the bulk of the underyearling rainbow trout population is minimized by size-dependent aggression and probably by size related habitat segregation. Intraspecific redd superimposition in rainbow trout augments size-related habitat and aggression segregation between underyearling brown trout and the bulk of the rainbow trout population by delaying peak emergence of the latter. The above arguments also apply to intraspecific competition between early and late emerging rainbow underyearlings.

7.4 INFLUENCE OF INTERSPECIFIC COMPETITION IN SCOTTS CREEK ON THE POPULATION EQUILIBRIUM OF BROWN AND RAINBOW TROUT IN LAKE ALEXANDRINA

I would now like to broaden this discussion by viewing competition within the confines of Scotts Creek, particularly competition for spawning space, in the wider context of its influence on the population equilibrium of brown and rainbow trout in Lake Alexandrina. It is surprising that in the almost one hundred years that brown and rainbow trout have lived in sympatry in Lake Alexandrina, brown trout have not been eliminated from the system, considering interspecific competition for spawning space, through redd superimposition, so severely debilitates reproductive success of that species. Some laboratory experiments with invertebrates in simple homogeneous environments have demonstrated

complete competitive exclusion (see Hardin 1960). However, if temporal variations are incorporated into such experiments, or into competition models, coexistence of competitors becomes a distinct possibility (see Grenney, Bella and Curl 1973, Koch 1974). The evidence for competitive exclusion in natural populations is at best "spotty and often almost anecdotal" (Wangersky 1978), and it is likely that competitive exclusion occurs rarely outside the laboratory (Birch 1957,1979, den Boer 1980, Hutchinson 1961, Miller 1967, Roughgarden 1976).

In the light of the preceding comments, and the evidence for the severity of interspecific competition for spawning space, it is interesting to speculate on the likelihood of competitive exclusion of brown trout from Lake Alexandrina, and to consider factors which may have allowed coexistence with rainbow trout in the past. The first point to consider is that the brown trout population may be maintained by input from other spawning grounds in which spawning success of early spawners is higher than in Scotts Creek. I consider this possibility unlikely. Of the other important spawning tributaries in the Lake Alexandrina system, Muddy Creek provides very limited and very poor physical spawning conditions and the Outlet Stream, although providing reasonably good physical conditions for spawning, also has a limited spawning area. Very few brown trout spawn in Muddy Creek (Moore et al. 1962, and personal observations). On the other hand possibly more brown trout now spawn in the Outlet Stream than in Scotts Creek. However, a large proportion of these brown trout appear to migrate upstream from Lake McGregor (Fig. 2.1) to spawn in the Outlet Stream (Moore et al. 1962). In both the Outlet Stream and Muddy Creek the spawning populations are dominated by rainbow trout which exhibit extended runs and generally spawn later than brown trout. Redd superimposition appears to be severe in both streams and hence, as in Scotts Creek, early spawners (including brown trout) would probably experience poor spawning success. A considerable amount of

lake edge spawning also occurs in Lake Alexandrina. While rainbow trout frequently are seen spawning around the lake edge, and presumably account for most of the redds observed, it is not known if brown trout also spawn in this manner in Lake Alexandrina.

Perhaps a more likely factor allowing maintenance of a viable population of brown trout is that occasionally, through reductions in numbers of late spawning rainbows or through later arrival of the peak rainbow trout spawning run, progeny of early spawners may experience a greater escapement from the redds. This could produce dominant year-classes of brown trout. Connell (1975) refers to this phenomenon in populations of the barnacle Balanus cariosus in which dominant year classes were produced by occasional escapes from intense juvenile predation by snails. Such intermittent recruitment appears to be common in severe predation situations, severe environments or in organisms at the extreme edge of their environmental range (Connell 1975). In this regard, redd superimposition could be included with predation situations since its effects on populations are similar. The long life span of brown trout (this species may exceed 13 years of age (Frost and Brown 1967)), its iteroparous reproductive strategy and its high fecundity would be advantageous for maintaining a population if intermittent recruitment occurs. In five years of personal occasional observations of early emerging fry in Scotts Creek, densities of brown fry appeared to be higher than normal in one year. This observation coincided with depressed numbers of rainbow trout spawning during late August and early September. "Species (i.e., populations of species (my brackets)) cannot coexist indefinitely because of the inevitability of random extinction ..." (Cole 1960). I think it is doubtful that in the long term, brown trout would be able to avoid random extinction if the species must rely on factors such as intermittent recruitment to maintain its population in Lake Alexandrina.

The answer to the question of coexistence of brown trout with rainbow trout in the past may lie in fisheries management practices carried out by the South Canterbury Acclimatization Society. Summaries of the Society's hatchery record sheets between the years 1932 and 1958 show that significant releases of fry of both species occurred regularly during this period. Usually between 10,000 and 215,000 brown fry and 96,000 and 536,000 rainbow fry were released into Lake Alexandrina each year. Annual reports of the Society for the period from the late 1950s to the late 1970s show that reasonably large scale releases of fry and hatchery-reared juveniles, and of fish salvaged from drought stricken rivers, were common. Between 1957 and 1962 artificial stocking concentrated mainly on fry releases, usually between 200,000 and 600,000 each year. These fish were mostly rainbow trout but significant numbers of brown trout were released also (e.g., up to 215,000 per year). Fry releases during this period were supplemented by small releases of hatchery-reared rainbow fingerlings (2000 to 5000 per year). Following a spawning survey of the three spawning streams of Lake Alexandrina carried out in 1962, Moore et al. (1962) concluded that they provided poor spawning conditions and redd superimposition was common. At that time, there was little spawning gravel in Scotts Creek and the bed was heavily silted. In compliance with Moore et al.'s recommendation to increase releases to about 25,000 yearling rainbow trout per year, stocking effort was increased in the late 1960s and 1970s. During the period from 1965 to 1978, 390,000 rainbow fry, 182,629 rainbow yearlings, 44,679 brown fingerlings and 6,368 quinnat salmon parr were released into the lake. This represents a significant input into the lake when compared with the present annual input from Scotts Creek of approximately 200,000 underyearlings, most of which are emergent fry. In subsequent years, following irregular releases of salvaged brown trout, the percent composition of brown trout in the angler's catch appeared to increase. I

strongly suspect that artificial stocking with brown trout was a significant factor in maintenance of that species' population in Lake Alexandrina in the past. I am also of the opinion that past fisheries management practices may have significantly influenced the composition and timing of the rainbow trout spawning run in Scotts Creek. In 1962 the rainbow trout spawning run exhibited a uniform temporal distribution (Appendix 3.3). The present temporal distribution, with its pronounced peak late in the season, appears to have developed within the past 10 years and its onset seems to have been coincidental with significant improvements made to the spawning bed of Scotts Creek by the South Canterbury Acclimatization Society. Improvements to the spawning bed were made in 1968 and 1970, and subsequently significant increases in densities of underyearlings in the stream were observed (annual reports of the South Canterbury Acclimatization Society between 1948 and 1981) . Observations of late peak spawning of rainbow trout followed in the early to middle 1970s. I suspect that prior to the improvement of the spawning bed success of natural propagation in Scotts Creek was low (as suggested by Moore et al. (1962)), and that returns of wild stock to spawn were small. Artificially propagated fish may have contributed significantly to the composition of the spawning run during that time. Such fish were not selected for late spawning; ova, for subsequent release as fry, were collected from Scotts Creek spawners at various times during the spawning season (J. Bull pers. comm.). Consequently these fish may have been responsible for the uniform temporal distribution of the spawning run. With the improvements to the spawning bed and subsequent improvement in natural propagation, returns of wild stock would account for a greater proportion of the spawning run. Since natural selection (acting through redd superimposition) for late spawning would occur the numbers of late spawners would be seen to increase. During the latter years of artificial

propagation the management practice of stripping late spawners for ova collection, for subsequent release as yearlings, would enhance the formation of the late spawning peak. Since 1978, when releases were discontinued and when further improvements were made to the spawning bed, the rainbow trout spawning run has been free from artificial perturbation and now exhibits a temporal pattern which is consistent with that expected in a wild stock limited by redd superimposition.

7.5 IMPLICATIONS FOR MANAGEMENT

The course of future management of the Lake Alexandrina fishery is dependent on whether a one or mixed species stock of salmonids is desired. If left in its present unperturbed state the fishery in all probability will become a monospecific stock of rainbow trout maintained well below carrying capacity by physical limitations of the spawning grounds. The brown trout has often been discriminated against by fisheries researchers and managers in mixed brown and rainbow trout fisheries (e.g., Lake Rotorua, New Zealand, see Burstall 1975; Convict Lake, California, see Nielson 1953; and to some extent, Lake Eucumbene, Australia, see Tilzey 1972). Often, this discrimination has resulted from observations or implications of apparent predation by brown trout on juvenile salmonids and evidence of low returns of this species to the angler. Consequently, it sometimes has been concluded that the brown trout is an unexploited burden on the biological economy of the lake (e.g., Nielson 1953). A problem with this "exploitation efficiency" approach is that it can be taken to the extreme as happens when optimal yield strategies are considered in the context of recreational fisheries (e.g., Allen 1951). This approach is irrelevant to most recreational salmonid fisheries, particularly in New Zealand, since maximum yield is

achieved at the expense of acceptable size. Rather, the aims of management for such fisheries as Lake Alexandrina should be to develop a balance between acceptable yield (catch rate) and large size, while attempting to provide a wide diversity of angling opportunities. In Lake Alexandrina, maintenance of a mixed fishery of brown and rainbow trout would achieve this latter aim, while large size of trout is naturally achieved by the physical limitations of the spawning grounds apparently maintaining the populations well below carrying capacity. A suitable rationale for future management of the Lake Alexandrina fishery might therefore be to attempt to maintain a mixed fishery of brown and rainbow trout, and concurrently to increase overall numbers but only to an extent such that mean adult size does not significantly deteriorate. These aims could be achieved through artificial propagation. However, this method requires continuous effort and might not be economically viable. Costs of stocking could be minimized if it was deemed sufficient simply to supplement natural fry output with artificially propagated fry rather than with larger hatchery reared juveniles. An alternative approach that could be considered, and which might prove to be economically more efficient in the long term, is to combine further enhancement of the spawning bed with artificial manipulation of the spawning runs to maximize fry output in Scotts Creek. It might be possible to enhance escapement of fry from the redds of brown trout and early spawning rainbow trout by denying later spawning rainbow trout access to the stream until September. The deposited embryos of the early spawning fish thus would be largely freed from disturbance by redd superimposition. Propagation of rainbow fry should not be impaired as a result of this manipulation since the very late spawners, which at present account for virtually all of the rainbow trout fry output, would still be free to spawn in the stream. In fact, such manipulation could potentially double the present output of fry from Scotts Creek, since early spawners might

then produce a similar quantity of fry to that now produced by late spawners. A bimodal emergence pattern of fry would be produced with enough temporal separation to minimize competition between underyearlings of the two groups within Scotts Creek, at least between fry and fingerlings. However, competition between the two groups of underyearlings might become important in late summer when late emerging fry have grown to a size where they require the fast,deep water habitat which would already be occupied by early emergent fish. Displacement of late emergent fish by early emergent fish might then occur, but should not seriously effect the survival potential of late emergent rainbow fry since (as has been shown) these stream resident fish represent only a small proportion of the late fry output from the stream.

I consider that the value of Scotts Creek to the Lake Alexandrina fishery lies in its potential for natural propagation of fry rather than in its capacity to rear juveniles. Management effort should concentrate on enhancing the spawning bed in an attempt to maximize natural fry propagation. Habitat improvement should be confined to providing temporary habitat only for underyearlings. Habitat for larger juveniles (i.e., large 0^+ fish, and 1^+ and 2^+ fish) should be kept at a minimum to minimize predation on fry. Such a programme could be supplemented with continual irregular releases of salvaged brown trout to boost the population of that species and ensure its continued presence in the fishery.

ACKNOWLEDGEMENTS

I thank my supervisors, Dr V.M. Stout and Dr C. McClay, for their assistance during this study. Dr Stout gave me a wealth of encouragement and counsel at all stages and Dr McClay gave excellent advise on experimental design and data analysis. I also thank my supervisors and Dr M. Winterbourn for their constructive critical reviews of the text.

I am indebted to Dr J.D. Hall (Oregon State University) for his advice during the early stages of the study.

My sincere thanks to South Canterbury Acclimatization Society field staff, Mr J. Bull and Mr G. McClintock, and also to Mr R. Hobbs for their invaluable assistance with field work and for their lively company which brightened many lonely months spent in the field. I am also grateful to Mr R. Thompson, Mr R. Holmes, Mr J. Cosgrove, Mr C. McGrath and Miss J. Davie for their assistance in the field. Thanks are due to Eric and Brian Davidson, Murray Heald, Gavin Robinson, Dave Greenwood, Mr A. Gall and my Father for their help in constructing the stream observation troughs.

I appreciated the technical computing assistance given by Richard Rowe and Tass Carrier. Dr M.H. Smith (Maths Department University of Canterbury) helped with some statistical problems.

I wish to thank Mrs Joan Buckley for her excellent work photographing and producing final prints of figures and Lyn Tomkies for typing the tables.

Thanks to Jim and Anne Murray for the use of their facilities and special thanks to "Red" and Carmel Watts for their generous hospitality which helped make bearable long periods of solitary life spent in the field.

I wish to acknowledge the South Canterbury Acclimatisation

Society which provided financial assistance for the study and accomadation in the field.

Finally I wish to thank Susan Hallas for her encouragement during the latter stages of thesis production and my Mother and Father for their love and support throughout the project.

REFERENCES

Alexander, D.R. & MacCrimmon, H.R. 1974. Production and movement of juvenile rainbow trout (Salmo gairdneri) in a headwater of Bothwells Creek, Georgian Bay, Canada. Journal of the Fisheries Research Board of Canada 31: 117-121.

Allen, K.R. 1951. The Horokiwi Stream. A study of a trout population. New Zealand Marine Department, Fisheries Bulletin No. 10.

Allen, K.R. 1962. The natural regulation of the salmonidae. New Zealand Science Review 20: 58-62.

Allen, K.R. & Cunningham, B.T. 1957. New Zealand Angling. 1947-1952. Results of the diary scheme. New Zealand Marine Department, Fisheries Bulletin No. 12.

Alley, T.R. 1982. Competition theory, evolution, and the concept of an ecological niche. Acta Biotheoretica 31: 165-179.

Alm, G. 1950. The sea-trout population in the Ava Stream. Report of the Institute of Freswater Research, Drottningholm 31: 26-56.

Alm, G. 1955. Artificial hybridization between different species of the salmon family. Report of the Institute of Freshwater Research, Drottningholm 36: 13-56.

Armstrong, R.W. & Argue, A.W. 1977. Trapping and coded-wire tagging of wild coho and chinook juveniles from the Cowichan River system, 1975. Fisheries and Environment, Canada, Fisheries and Marine Service Technical Report Series PAC/T-77-14.

Au, D.W.K. 1971. Population dynamics of the coho salmon and its response to logging in three coastal streams. Unpubl. Ph.D. thesis, Oregon State University, Oregon.

Backiel, T. & LeCren, E.D. 1967. Some density relationships for fish population parameters. pp. 261-294. In: Gerking, S.D. (Ed.), The Biological Basis of Freshwater Fish Production. Blackwell Scientific Publications, Oxford.

Backiel, T. & LeCren, E.D. 1978. Some density relationships for fish population parameters. pp. 279-302. In: Gerking, S.D. (Ed.), Ecology of Freshwater Fish Production. Blackwell Scientific Publications, Oxford.

Ball, O.P. & Cope, O.B. 1961. Mortality studies on cutthroat trout in Yellowstone Lake. U.S. Fish and Wildlife Service. Research report 55: 1-62.

Bams, R.A. 1969. Adaptations of sockeye salmon associated with incubation in stream gravels. pp. 71-87. In: Northcote, T.G. (Ed.), Symposium on Salmon and Trout in Streams. H.R. MacMillan Lectures in Fisheries. University of British Columbia, Vancouver, Canada.

Benson, N.G. 1953. The importance of ground water to trout populations in the Pidgeon River, Michigan. Transactions of the Eighteenth North American Wildlife Conference 269-281.

Benson, N.G. 1960. Factors influencing production of immature cutthroat trout in Arnica Creek, Yellowstone Park. Transactions of the American Fisheries Society 89: 168-175.

Birch, L.C. 1957. The meanings of competition. The American Naturalist 91: 5-18.

Birch, L.C. 1979. The effects of species of animals which share common resources on another's distribution and abundance. Fortschritte der Zoologie 25: 197-221.

Birch, L.C. & Ehrlich, P.R. 1967. Evolutionary history and population biology. Nature 214: 349-352.

Blanc, J.M. & Chevassus, B. 1979. Interspecific hybridization of salmonid fish. I. Hatching in F1 generation hybrids. Aquaculture 18: 21-34.

Boreman, J. 1981. Characteristics of fall and spring migrant rainbow trout in Coyugu Inlet, New York. New York Fish and Game Journal 28: 100-107.

Braddock, J.C. 1945. Some aspects of the dominance-subordination relationship in the fish Platypoecilus maculatus. Physiological Zoology 18: 176-195.

Braddock, J.C. 1949. The effects of prior residence upon dominance in the fish Platypoecilus maculatus. Physiological Zoology 23: 161-169.

Briggs, J.C. 1953. The behaviour and reproduction of salmonid fishes in a small coastal stream. California Fish and Game, Fisheries Bulletin No. 94.

Burstall, P.J. 1975. Sport fisheries. pp. 308-318. In: Jolly, V.H. & Brown, J.M.A. (Eds.) New Zealand Lakes. Auckland University Press, New Zealand.

Buss, K. & Wright, J.E. 1956. Results of species hybridization within the salmonidae. Progressive Fish Culturist 18: 149-158.

Cairns, D. 1942. Life history of the two species of New Zealand eels. New Zealand Journal of Science and Technology 23: 53-72.

Case, T.J. & Gilpin, M.E. 1974. Interference competition and niche theory. Proceedings of the Natural Academy of Science U.S.A. 71: 3073-3077.

Chapman, D.W. 1962. Aggressive behaviour in juvenile coho salmon as a cause of emigration. Journal of the Fisheries Research Board of Canada 19: 1047-1080.

Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. The American Naturalist 100: 345-357.

Chapman, D.W. & Bjornn, T.C. 1968. Distribution of salmonids in streams, with special reference to food and feeding. pp. 153-176. In: Northcote, T.G. (Ed.) Symposium on Salmon and Trout in Streams. H.R. MacMillan Lectures in Fisheries, University of British Columbia. 388pp.

Chapman, D.W. 1978. Production. pp. 202-217. In: Bagenal, T. (Ed.), Methods for the Assessment of Fish Production in Freshwaters. 3rd Edn. IBP Handbook No. 3. Blackwell Scientific Publications, Oxford.

Cole, L.C. 1960. Competitive exclusion. Science 132: 348-349.

Cole, K.S. 1976. Social behaviour and social organization of young trout, Salmo gairdneri, of hatchery origin. Unpubl. M.Sc. thesis, Zoology Department, University of Guelph, Guelph, Ontario.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. pp. 460-490. In: Cody, M.L. & Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Harvard University Press, Cambridge, Massachusetts.

Connell, J.H. 1983. On the prevalence and relative importance of intersecific competition: evidence from field experiments. The American Naturalist 122: 661-696.

Connor, E. & Simberloff, D. 1979. The assembly of species communities; chance or competition? Ecology 60: 1132-1140.

Crisp, D.T. 1980. Prediction of eyeing, hatching and swim-up times for brown trout and Atlantic salmon from water temperatures. Unpubl. report, Freswater Biological Association, Teesdale Unit.

Crisp, D.T. 1981. A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. Freshwater Biology 11: 361-368.

Crisp, D.T. & Ottaway, E.M. 1981. Comparison of observed and predicted dates of eyeing, hatching and swim-up for brown trout and Atlantic salmon. Unpubl. report, Freshwater Biological Association, Teesdale Unit.

Crombie, A.C. 1944. On intraspecific and interspecific competition in larvae of graminivorous insects. Journal of Experimental Biology 20: 135-151.

Crombie, A.C. 1945. On competition between different species of graminivorous insects. Proceedings of the Royal Society B, 132: 362-395.

Crombie, A.C. 1946. Further experiments on insect competition. Proceedings of the Royal Society London B 133: 76-109.

Cuinat, R. & Heland, M. 1979. Observations sur la devalaison d alevins de Truite commune (Salmo trutta L.) dans le Lissuraga. Bulletin Francais de Pisciculture 274: 1-17.

Culver, D.C. 1975. Interaction between competition and predation in cave stream communities. International Journal of Speleology 7: 229-245.

den Boer, P.J. 1980. Exclusion or coexistence and the taxonomic or ecological relationships between species. Netherlands Journal of Zoology 30: 278-306.

Diamond, J.M. 1978. Niche shifts and the rediscovery of interspecific competition. American Scientist 66: 322-331.

Egglishaw, H.J. 1967. The food, growth and population structure of salmon and trout in two streams in the Scottish Highlands. Freshwater and Salmon Fisheries Research 38: 1-32.

Egglishaw, H.J. 1970. Production of salmon and trout in a stream in Scotland. Journal of Fish Biology 2: 117-136.

Egglishaw, H.J. & Shackley, P.E. 1977. Growth, survival and production of juvenile salmon and trout in a Scottish stream, 1966-75. Journal of Fish Biology 11: 647-672.

Egglishaw, H.J. & Shackley, P.E. 1980. Survival and growth of salmon, Salmon salar (L.), planted in a Scottish stream. Journal of Fish Biology 16: 565-584.

Egglishaw, H.J. & Shackley, P.E. 1982. Influence of water depth on dispersion of juvenile salmonids, Salmo salar L., in a Scottish stream. Journal of Fish Biology 21: 141-155.

Elliott, J.M. 1966. Downstream movements of trout fry Salmo trutta in a Dartmoor stream. Journal of the Fisheries Research Board of Canada 23: 157-159.

Elton, C. 1946. Competition and stucture of ecological communities. Journal of Animal Ecology 15: 54-68.

Erman, D.C. & Leidy, G.R. 1975. Downstream movement of rainbow trout fry in a tributary of Saghen Creek, under permanent and intermittent flow. Transactions of the American Fisheries Society 104: 467-473.

Everest, F.H., Jr. 1971. An ecological and fish cultural study of summer steelhead in the Rogue River, Oregon Annual Progress Report. Anadromous Fish Project. AFS-31. Oregon State Game Commission.

Everest, F.H. & Chapman, D.W. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 29: 91-100.

Fabricius, E. 1953. Aquarium observations on the spawning behaviour of the char, Salvelinus alpinus. Report of the Institute of Freshwater Research, Drottningholm 34: 14-48.

Foerster, R.E. 1968. The Sockeye Salmon, Oncorhynchus nerka. Fisheries Research Board of Canada, Ottawa 1968, Bulletin 162.

Frost, W.E. & Brown, M.E. 1967. The Trout. Collins, London.

Gair, H.S. 1967. Geological map of New Zealand 1:250,000

Gangmark, H.A. & Bakhala, R.E. 1960. A comparative study of unstable and stable (artificial channel) spawning streams for incubating king salmon at Mill Creek. California Fish and Game 46: 151-164.

Gardiner, W.R. & Geddes, P. 1980. The influence of body composition on the survival of juvenile salmon. Hydrobiologia 69: 67-72.

Gause, G.F. 1934. The Struggle for Existence. Williams and Wilkins, Baltimore. 163pp.

Gibson, R.J. 1966. Some factors influencing the distributions of brook trout and young Atlantic salmon. Journal of the Fisheries Research Board of Canada 23: 1977-1980.

Gibson, R.J. 1981. Behavioural interactions between coho salmon (Salvelinus kisutch), Atlantic salmon (Salmo salar), brook trout (Salvelinus fontinalis), and steelhead trout (Salmo gairdneri), at the juvenile fluviatile stages. Canadian Technical Report of Fisheries and Aquatic Sciences No. 1029. 116pp.

Giesel, J.T. 1974. The Biology and Adaptability of Natural Populations. C.V. Mosby, St. Louis.

Gilbert, C.H. & Rich, W.H. 1927. Investigations concerning the red-salmon runs into the Karluk River, Alaska. Bulletin, U.S. Bureau of Fisheries 43: 1-69. (Document No. 1021.)

Glova, G.J. 1978. Pattern and mechanism of resource partitioning between stream populations of juvenile coho salmon (Oncorhynchus kisutch) and coastal cutthroat trout (Salmo clarki clarki). Unpubl. Ph.D. thesis, Department of Zoology, University of British Columbia, Vancouver, Canada. 185pp.

Grant, P.R. 1972. Interspecific competition among rodents. Annual Review of Ecology and Systematics 3: 79-106.

Greenberg, B. 1947. Some relations between territory, social heirarchy and leadership in the green sunfish (Lepomis cyanellus). Physiological Zoology 20: 269-299.

Grenney, W.J., Bella, D.A. & Curl, H.C. 1973. A theoretical approach to interspecific competition in phytoplankton communities. The American Naturalist 107: 405-425.

Griffith, J.S.,Jr. 1972. Comparative behaviour and habitat utilization of brook trout (Salvelinus fontinalis) and cutthroat trout (Salmo clarki) in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada 29: 265-273.

Griffiths, W.E. 1976. Feeding and gastric evacuation in perch (Perca fluviatilis L.). Mauri Ora 4: 19-34.

Grinnell, J. 1904. The origin and distribution of the chestnut-backed chickadee. Auk 21: 364-382.

Grinnell, J. 1908. The biota of the San Bernardino Mountains. University of California Publications in Zoology 5: 1-170.

Hanavan, M.G. & Skud, B.E. 1954. Intertidal spawning of pink salmon. U.S. Fish and Wildlife Service, Fisheries Bulletin 95: 167-185.

Hansen, E.A. 1975. Some effects of ground water on brown trout redds. Transactions of the American Fisheries Society 104: 100-110.

Hardin, G. 1960. The competitive exclusion principle. Science 131: 1292-1297.

Harrison, J.O. 1964. Factors affecting the abundance of Lepidoptera in banana plantations. Ecology 45: 508-519.

Hart, J.L. 1973. Pacific Fishes of Cananda. Fisheries Research Board of Canada, Ottawa 1973, Bulletin 1980.

Hartman, G.F. 1963. Observations on behaviour of juvenile brown trout in a stream aquarium during winter and spring. Journal of the Fisheries Research Board of Canada 20: 769-787.

Hartman, G.F. 1965. The role of behaviour in the ecology and interaction of underyearling coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). Journal of the Fisheries Research Board of Canada 22: 1035-1081.

Hartman, G.F. & Galbraith, D.M. 1970. The Reproductive Environment of the Gerard Stock Rainbow Trout. Fisheries Management Publication No. 15. University of Guelph, Ontario.

Hartman, W.L. 1958. Biology and vital statistics of rainbow trout in the Finger Lakes region, New York. Unpubl. Ph.D. thesis, Cornell University. 104pp.

Hartman, W.L., Strickland, C.W. & Hoopes, D.T. 1962. Survival and behaviour of sockeye salmon fry migrating into Brooks Lake, Alaska. Transactions of the American Fisheries Society 91: 133-139.

Healey, M.C., Jordan, F.D. & Hungar, R.M. 1976. Laboratory and field evaluating of fluorescent grit as a marking material for juvenile salmonids. Fisheries Research Board of Canada, Manuscript Report Series No. 1392.

Heland, M. 1980a. La devalaison des alevins de truite commune, Salmo trutta L. I. Caracterisation en milieu artificiel. Annales de Limnologie 16: 233-245.

Heland, M. 1980b. La devalaison des alevins de truite commune, Salmon trutta L. II. Activite des alevins <<devalants>> compares aux sedentaires. Annales de Limnologie 16: 247-254.

Helle, J.H. 1970. Biological characteristics of intertidal and freshwater spawning pink salmon at Olsen Creek, Prince William Sound, Alaska, 1962-1963. U.S. Fish and Wildlife Service Special Scientific Report Fisheries 602. 19pp.

Helle, J.H., Williamson, R.S. & Bailey, J.E. 1964. Intertidal ecology and life history of pink salmon at Olsen Creek, Prince William Sound, Alaska. U.S. Fish and Wildlife Service Special Scientific Report Fisheries 483. 26pp.

Hoar, W.S. 1951. The behaviour of chum, pink and coho salmon in relation to their seaward migration. Journal of the Fisheries Research Board of Canada 8: 241-263.

Hoar, W.S. 1956. The behaviour of migrating pink and chum salmon fry. Journal of the Fisheries Research Board of Canada 13: 309-325.

Hoar, W.S. 1958. The evolution of migratory behaviour among juvenile salmon of the genus Oncorhynchus. Journal of the Fisheries Research Board of Canada 15: 391-428.

Hobbs, D.F. 1937. Natural reproduction of quinnat salmon, brown trout and rainbow trout in certain New Zealand waters. New Zealand Marine Department, Fisheries Bulletin No. 6.

Hobbs, D.F. 1940. Natural reproduction of trout in New Zealand and its relation to density of populations. New Zealand Marine Department, Fisheries Bulletin No. 8.

Hobbs, D.F. 1948. Trout fisheries in New Zealand, their development and management. New Zealand Marine Department, Fisheries Bulletin No. 9.

Hofer, Br. 1909. Die Susswasserfische von Mittel-Europa. Verlag Schluter & Mass. Halle am S. 558pp.

Hopkins, C.L. 1970. Some aspects of the bionomics of fish in a brown trout nursery stream. Fisheries Research Division, New Zealand Marine Department. Fisheries Research Bulletin No. 4.

Hopkins, C.L. 1981. Juvenile production and yield in quinnat salmon. pp. 11-14. In: Proceedings of the Salmon Symposium. Fisheries Research Division. New Zealand Ministry of Agriculture and Fisheries, Occasional Publication No. 30.

Hunt, P.C. 1972. Observations of the spawning migrations of brown trout from Lake Taupo, New Zealand. M.S. copy.

Hunt, R.L. 1965. Dispersal of wild brook trout during their first summer of life. Transactions of the American Fisheries Society 94: 186-188.

Hunter, J.G. 1959. Survival and production of pink and chum salmon in a coastal stream. Journal of the Fisheries Research Board of Canada 16: 835-886.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 415-427.

Hutchinson, G.E. 1961. The paradox of the plankton. The American Naturalist 95: 137-145.

Hutchinson, G.E. 1978. An Introduction to Population Ecology. Yale University Press, London. 260pp.

Hynes, H.B.N. 1950. The food of freshwater sticklebacks (Gasterostous aculeatus and Pygosteus pungitiu), with a review of methods used in studies of the food of fishes. Journal of Animal Ecology 19: 35-58.

Irvine, J.R. 1978. The rearing and feeding ecology of juvenile rainbow trout from a large lake-fed river. Unpubl. M.Sc. thesis. University of British Columbia, Vancouver.

Irwin, J. 1978. Lake Alexandrina, Bathymetry 1:12,000. New Zealand Oceanographic Institute Chart, Lake Series.

Iwamoto, R.N., Salo, E.O., Madej, M.A. & McComas, R.L. 1978. Sediment and water quality: a review of the literature including a suggested approach for water quality criteria. U.S. Environmental Protection Agency, Seattle, Washington. EPA 910/9-78-048.

Johnson, W.E. 1965. On mechanisms of self-regulation of population abundance in Oncorhynchus nerka. Mitteilungen der Internationalen Vereinigung fur theoretische und angewundte Limnologie 13: 88-105.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar L. and S. trutta L.). Report. Institute of Freswater Research, Drottningholm 39: 55-98.

Kaufmann, J.H. 1983. On the definitions and functions of dominance and territory. Biological Review 58: 1-20.

Kelso, B.W., Northcote, T.G. & Wehrhahn, C.F. 1981. Genetic and environmental aspects of the response to water current by rainbow trout (Salmo gairdneri) originating from outlet and inlet streams of two lakes. Canadian Journal of Zoology 59: 2177-2185.

Kennedy, G.J.A. 1982. Factors affecting the survival and distribution of salmon (Salmo salar L.) stocked in upland trout (Salmo trutta L.) streams in Northern Ireland. EIFAC, 12th session, Symposium on Stock Enhancement in the Management of Freshwater Fisheries. Budapest 1982.

Kennedy, J.G.A. & Strange, C.D. 1980. Population changes after two years of salmon (Salmo salar L.) stocking in upland trout (Salmo trutta L.) streams. Journal of Fish Biology 17: 577-586.

Kennedy, G.J.A. & Strange, C.D. 1982. The distribution of salmonids in upland streams in relation to depth and gradient. Journal of Fish Biology 20: 579-591.

Kleenleyside, M.H.A. 1962. Skin-diving observations of Atlantic salmon and brook trout in the Miramichi, N.B. Journal of the Fisheries Research Board of Canada 19: 625-634.

Kleenleyside, M.H.A. 1979. Diversity and Adaptation in Fish Behaviour. Springer-Verlag, Berlin.

Kleenleyside, M.H.A. & Yamamoto, F.T. 1962. Territorial behaviour of Atlantic salmon (Salmo salar). Behaviour 19: 139-169.

Koch, A.L. 1974. Coexistence resulting from an alteration of density-dependent and density-independent growth. Journal of Theoretical Biology 44: 373-386.

Krebs, C.J. 1978. Ecology. The Experimental Analysis of Distribution and Abundance. 2nd edition. Harper & Row, New York. 678pp.

Krogius, F.V. & Krokhin, E.M. 1948. (On the production of young sockeye salmon (Oncorhynchus nerka Walb.).) Investiia TINRO 28: 3-27. (FRB Translation No. 109.)

Krogius, F.V. 1951. (On the dynamics of abundance of the sockeye salmon (Oncorhynchus nerka, Walbaum).) Investiia TINRO, 35: Vladivostok. (FRB Translation No. 101.)

Krokhin, E.M. & Krogius, F.V. 1933. Spawning grounds and the spawning of red salmon in the basin of Lake Kourilsky, Kamchatka. Translation by Julia Krenov in Fisheries Oceanography Library, Unversity of Washington, Seattle. 40pp.

Kuznetsov, I.I. 1928. Nekotorye nablyudeniya nad razmnozheniem Amurskikhii Kamchtskikh lososei (Some observations on spawning of the Amur and Kamchatka salmons). Izv. Tikhookeansk. Nauch. promysl. Sta. 2: 1-195. (Fisheries Research Board of Canada Translation Series No. 22.)

Kwain, W.H. 1971. Life history of rainbow trout (Salmo gairdneri) in Batchawana Bay, eastern Lake Superior. Journal of the Fisheries Research Board of Canada 28: 771-775.

Lack, D. 1945. The ecology of closely related species with special reference to cormorant (Phalacrocorax carbo) and shag (P. aristotelis). Journal of Animal Ecology 14: 12-16.

Lack, D. 1947. Darwins Finches. Cambridge University Press, New York.

Laird, M.G. & Lewis, D.W. 1976. Sedimentary geology of Precambrian to Quaternary rocks, South Island (Northern Part), New Zealand. 25th I.G.C. Excursion Guide No. 58C: 12-14.

Larkin, P.A. 1956. Interspecific competition and population control in freshwater fish. Journal of the Fisheries Research Board of Canada 13: 327-342.

Latta, W.C. 1962. Periodicity of mortality of brook trout during first summer of life. Transactions of the American Fisheries Society 91: 408-411.

LeCren, E.D. 1961. How many fish survive ? River Boards Association Yearbook London 9: 57-64.

LeCren, E.D. 1962. The efficiency of reproduction and recruitment in freshwater fish. pp. 283-296. In: LeCren, E.D. & Holdgate, M.W. (Eds.), The Exploitation of Natural Animal Populations. Blackwell Scientific Publications, Oxford.

LeCren, E.D. 1965. Some factors regulating the size of populations of freshwater fish. Mitteilungen der Internationalen Vereinigung fur theoretische und angewundte Limnologie 13: 88-105.

Levins, R. 1968. Evolution in Changing Environments. Princeton University Press, Princeton.

Lewis, S.L. 1967. Physical factors influencing populations in pools of a trout stream. Unpubl. M.Sc. thesis, Montana State University.

Lindsey, Cc., Northcote, T.G. & Hartman, G.F. 1959. Homing of rainbow trout to inlet and outlet spawning streams at Loon Lake, British Columbia. Journal of the Fisheries Research Board of Canada 16: 695-719.

Lister, D.B. & Genoe, H.S. 1970. Stream habitat utilization by cohabiting underyearlings of chinook (Oncorhynchus tshawytscha) and coho (O. kisutch) salmon in the Big Qualicum River, British Columbia. Journal of the Fisheries Research Board of Canada 27: 1215-1224.

Lister, D.B. & Walker, C.E. 1966. The effect of flow on freshwater survival of chum, coho, and chinook salmon in the Big Qualicum River. Canadian Fish Culturist 37: 3-25.

Lotka, A.J. 1925. Elements of Physical Biology. Williams and Wilkins, Baltimore. (Reprinted 1956 by Dover Publications, New York as Elements of Mathematical Biology).

MacCrimmon, H.R. 1971. World distribution of rainbow trout (Salmo gairdneri). Journal of the Fisheries Research Board of Canada 28: 663-704.

MacCrimmon, H.R. & Marshall, T.L. 1968. World distribution of brown trout, Salmo trutta. Journal of the Fisheries Research Board of Canada 25: 2527-2548.

MacKinnon, D. & Brett, J.R. 1955. Some observations on the movement of Pacific salmon fry through a small impounded water basin. Journal of the Fisheries Research Board of Canada 12: 362-368.

MacPhee, C. 1961. An experimental study of competition for food in fish. Ecology 42: 666-681.

Manning, A. 1979. An Introduction to Animal Behaviour. Edward Arnold Ltd., London. 329pp.

Mansergh, G.D. 1973. Quaternary of the Mackenzie Basin. INQUA Guidebook for Excursion 7, IX INQUA Congress, Christchurch: 1031-1045.

Mason, J.C. 1969. Hypoxial stress prior to emergence and competition among coho salmon fry. Journal of the Fisheries Research Board of Canada 26: 63-91.

Mason, J.C. 1975. Seaward movement of juvenile fishes, including lunar periodicity in the movement of coho salmon (Oncorhynchus kisutch) fry. Journal of the Fisheries Research Board of Canada 32: 2542-2547.

Mason, J.C., Brynildson, O.M. & Degurse, P.E. 1967. Comparative survival of wild and domestic strains of brook trout in streams. Transactions of the American Fisheries Society 96: 313-319.

Mason, J.C. & Chapman, D.W. 1965. Significance of early emergence, environmental rearing capacity and behavioural ecology of juvenile coho salmon in stream channels. Journal of the Fisheries Research Board of Canada 22: 173-190.

Mathisen, O.A. 1962. The effect of altered sex ratios on the spawning of red salmon. pp. 137-245. In: Studies of Alaska red salmon, Vol. 1. University of Washington Publications in Fisheries., New Series.

May, R.M. 1981. (Ed.) Theoretical Ecology. Blackwell Scientific Publications, Oxford. 489pp.

McFadden, J.T. 1961. A population study of the brook trout Salvelinus fontinalis. Wildlife Monographs 7. 73pp.

McFadden, J.T. 1968. Dynamics and regulation of salmonid populations in streams. pp. 313-332. In: Northcote, T.G. (Ed.), Symposium on Salmon and Trout in Streams. H.R. MacMillan Lectures in Fisheries. University of British Columbia, Vancouver, Canada.

McNeil, W.J. 1962. Mortality of pink and chum salmon eggs and larvae in southeast Alaska streams. Unpubl. Ph.D. thesis, University of Washington, Seattle, U.S.A.. 270pp.

McNeil, W.J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. Journal of the Fisheries Research Board of Canada 21: 1385-1396.

McNeil, W.J. 1967. Randomness in distribution of pink salmon redds. Journal of the Fisheries Research Board of Canada 24: 1629-1634.

Merrell, T.R. Jr. 1962. Freshwater survival of pink salmon at Sashin Creek, Alaska. pp. 59-72. In: Wilimovsky, N.J. (Ed.), A Symposium on Pink Salmon. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.

Miller, R.B. 1957. Permanence and size of home territory in stream-dwelling cutthroat trout. Journal of the Fisheries Research Board of Canada 14: 687-691.

Miller, R.B. 1958. The role of competition in the mortality of hatchery trout. Journal of the Fisheries Research Board of Canada 15: 27-56.

Miller, R.S. 1967. Pattern and process in competition. Advances in Ecological Research 4: 1-74.

Miller, R.S. 1969. Competition and species diversity. Brookhaven Symposia in Biology 22: 63-70.

Milner, N.J., Scullion, J., Carling, P.A. & Crisp, D.T. 1981. The effects of discharge on sediment dynamics and consequent effects on invertebrates and salmonids in upland rivers. Advances in Applied Biology 6: 153-198.

Moore, E., Cunningham, B.T., Baw, E.D. & Lewall, E.G. 1962. Spawning survey of Lake Alexandrina and adjacent waters. New Zealand Marine Department, Freshwater Advisory Service investigaton report No. 40. 37pp.

Morse, D.H. 1974. Niche breadth as a function of social dominance. The American Naturalist 108: 818-830.

Mottley, C. McC. 1932. The propagation of trout in the Kamloops district, British Columbia. Transactions of the American Fisheries Society 62: 144-151.

Mottley, C. McC. 1938. Loss of weight by rainbow trout at spawning time. Transactions of the American Fisheries Society 67: 207-210.

Moring, J.R. & Lantz, R.L. 1975. The Alsea watershed study: effects of logging on the aquatic resources of three headwater streams of the Alsea River, Oregon. Part 1 biological studies. Oregon wildlife Commission Fisheries Research Report No. 9. 66pp.

Mortensen, E. 1977a. The population dynamics of young trout (Salmo trutta L.) in a Danish brook. Journal of Fish Biology 10: 23-33.

Mortensen, E. 1977b. Population, survival, growth and production of trout (Salmo truttaL.) in a small Danish stream. Oikos 28: 9-15.

Mortensen, E. 1977c. Density-dependent mortality of trout fry (Salmo trutta L.) and its relationship to management of small streams. Journal of Fish Biology 11: 613-617.

Mundie, J.H. 1974. Optimization of the salmonid nursery stream. Journal of the Fisheries Research Board of Canada 31: 1827-1837.

Murray, B.G., Jr. 1971. The ecological consequences of interspecific territorial behaviour in birds. Ecology 52: 414-423.

Neave, F. 1955. Notes on the seaward migration of pink and chum salmon fry. Journal of the Fisheries Research Board of Canada 12: 369-374.

Neill, W.E. 1974. The community matrix and interdependence of the competition coefficients. The American Naturalist 108: 399-408.

Newman, M.A. 1956. Social behaviour and interspecific competition in two trout species. Physiological Zoology 29: 64-81.

Nielson, R.S. 1953. Should we stock brown trout ? The Progressive Fish Culturist 15: 125-126.

Nilsson, N.-A. 1956. Om konkurrensen i naturen. Zoologisk Revy 1956: 40-47.

Nilsson, N.-A. 1965. Food segregation between salmonid species in North Sweden. Report of the Institute of Freshwater Research, Drottningholm 46: 58-73.

Noakes, L.G. 1978. Social behaviour as it influences fish production. pp. 360-382. In: Gerking, S.D. (Ed.), Ecology of Freshwater Fish Production. Blackwell Scientific Publications, Oxford.

Northcote, T.G. 1962. Migratory behaviour of juvenile rainbow trout (Salmo gairdneri) in outlet and inlet streams of Loon Lake, British Columbia. Journal of the Fisheries Research Board of Canada 19: 201-270.

Northcote, T.G. 1967. The relation of movements and migrations to production in freshwater fishes. pp. 315-344. In: Gerking, S.D. (Ed.), The Biological Basis of Freshwater Fish Production. Blackwell Scientific Publications, Oxford.

Northcote, T.G. 1978. Migratory strategies and production in freshwater fishes. pp. 326-359. In: Gerking, S.D. (Ed.) Ecology of Freshwater Fish Production. Blackwell Scientific Publications, Oxford.

O'Connor, K.F. 1975. An introduction to The Waitaki. New Zealand Man and the Biosphere Report No. 1. Tussock Grasslands and Mountain Lands Institute, Lincoln College, Canterbury, New Zealand.

Odum, E.P. 1971. Fundamentals of Ecology. 3rd edition. W.B. Saunders Co., London. 574pp.

Onodera, K. 1962. Carrying capacity in a trout stream. Bulletin of the Freshwater Fisheries Research Laboratory (Tokyo) 12: 1-41.

Ottaway, E.M. & Clarke, A. 1981. A preliminary investigation into the vulnerability of young trout (Salmo trutta L.) and Atlantic salmon (S. salar L.) to downstream displacement by high water velocities. Journal of Fish Biology 19: 135-145.

Paine, R.T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52: 1096-1106.

Park, T. 1948. Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, Tribolium confusum (Duval) and Tribolium castaneum (Herst.). Ecological Monographs 18: 267-307.

Park, T. 1954. Experimental studies of interspecies competition. II. Temperature, humidity, and competition in two species of Tribolium. Physiological Zoology 27: 177-238.

Park, T. 1962. Beetles, competition, and populations. Science 138: 1369-1375.

Peterson, R.H.. 1978. Physical characteristics of Atlantic salmon spawning gravel in some New Brunswick streams. Fisheries Marine Service technical Report. 785pp.

Phinney, D.E., Miller, D.M. & Dahlberg, M.L. 1967. Mass-marking young salmonids with fluorescent pigment. Transactions of the American Fisheries Society 96: 157-162.

Pianka, E.R. 1981. Competition and Niche Theory. pp. 167-196. In: May, R.M. (Ed.), Theoretical Ecology. Blackwell Scientific Publications, Oxford. 489pp.

Pitcher, T.J. & MacDonald, P.D.M. 1973. A numerical integration method for fish population fecundity. Journal of Fish Biology 5: 549-553.

Pribble, J. 1976. Pressure spray marking of fish with granular dyes. Oregon Department of Fish and Wildlife. M.S. copy.

Pritchard, A.L. 1947. Efficiency of natural propagation of Pacific salmon. Canadian Fish Culturist 1: 22-26.

Reed, R.J. 1967. Observations of fishes associated with spawning salmon. Transactions of the American Fisheries Society 96: 62-67.

Reimers, P.E. 1970. Behaviour troughs with simulated redds to study recently emerged salmon fry. Oregon Fish Commission Research Report 2: 96-99.

Reimers, P.E. 1973. The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Oregon Fish Commission Research Report No. 4. 43pp.

Ricker, W.E. 1973. Linear regressions in fishery research. Journal of the Fisheries Research Board of Canada 30: 409-434.

Ricker, W.E. 1979. Growth rates and models. pp. 677-743. In: Hoar, W.S. (Ed.), Fish Physiology. New York Academic Press, New York.

Rinne, W.E. & Deacon, J.E. 1973. Fluorescent pigment and immersion stain marking techniques for Lepidomeda mollispinis and Cyprinodon nevadensis. Transactions of the American Fisheries Society 102: 459-462.

Roughgarden, J. 1976. Resource partitioning among competing species. A coevolutionary approach. Theoretical Population Biology 9: 388-424.

Saunders, J.W. & Smith, M.W. 1962. Physical alterations of stream habitat to improve brook trout production. Transactions of the American Fisheries Society 91: 185-188.

Scheer, B.T. 1939. Homing instinct in salmon. Quarterly review of Biology 14: 408-430.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

Schoener, T.W. 1982. The controversy over interspecific competition. American Scientist 70: 586-595.

Schoener, T.W. 1983. Field experiments on interspecific competition. The American Naturalist 122: 240-285.

Schroder, S.L. 1973. Effects of density on the spawning success of chum salmon (Oncorhynchus keta) in an artificial spawning channel. Unpubl. M.Sc. thesis, University of Washington, Seattle. 78pp.

Scott, D. & Fraser, J.C. 1978. The origins of rainbow trout, Salmo gairdneri Richardson, in New Zealand. California Fish and Game 64: 210-218.

Seegrist, D.W. & Gard, R. 1972. Effects of floods on trout in Saghen Creek, California. Transactions of the American Fisheries Society 101: 464-478.

Semko, R.S. 1939. Kamchatskaya gorbusha (Kamchatka pink salmon). Izvestiya TINRO (Bulletin of TINRO) 16.

Semko, R.S. 1954. Zapasy zapadnokamchatskikh lososei i ikh promyslovoe isopol 'zovanie (The stocks of West Kamchatka salmon and their commercial utilization). Inst. Ryb. Khoz-Okeanogr. 41: 3-109. (Translation, Fisheries Research Board of Canada Biological Station, Nanaimo, British Columbia, Translation Series No. 288.)

Shapovalov, L. & Taft, A.C. 1954. The life histories of the steelhead rainbow trout (Salmo gairdneri gairdneri) and silver salmon (Oncorhynchus kisutch) with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game, Fish Bulletin, No. 98. 375pp.

Shirazi, M.A. & Seim, W.K. 1979. A stream systems evaluation - An emphasis on spawning habitat for salmonids. Corvalis Environmental Research Lab., Corvalis, Oregon. EPA-600/3-79-109.

Slaney, P.A. & Northcote, T.G. 1974. Effects of prey abundance on density and territorial behaviour on young rainbow trout (Salmo gairdneri) in laboratory stream channels. Journal of the Fisheries Research Board of Canada 31: 1201-1209.

Smirnov, A.I. 1960. (The characteristics of the biology of reproduction and development of the coho- Oncorhynchus kisutsh (Walbaum).) Vestnik Moskovskogo University 1960, Series 6 (Biology), 1: 9-19. (FRB Translation No. 287.)

Sokal, R.R. & Rohlf, F.J. 1969. Biometry. The principles and practice of statistics in biological research. Freeman & Co., San Francisco. 776pp.

Stauffer, T.M. 1972. Age, growth, and downstream migration of juvenile rainbow trout in a Lake Michigan tributary. Transactions of the American Fisheries Society 101: 18-28.

Stein, R.A., Hall, J.D. & Reimers, P.E. 1972. Social interaction between juvenile coho (Oncorhynchus kisutch) and fall chinook salmon (O. tshawytscha) in Sixes River, Oregon. Journal of the Fisheries Research Board of Canada 29: 1737-1748.

Stokell, G. 1949. The numerical characteristics of five hybrid trout. Records of Canterbury (N.Z.) 5: 209-212.

Stringer, G.E. & Hoar, W.S. 1955. Aggressive behaviour of underyearling Kamloops trout. Journal of Zoology 33: 148-160.

Stuart, T.A. 1953. Water currents through permeable gravels and their significance to spawning salmonids. Nature, London 172: 407-408.

Stuart, T.A. 1954. Spawning sites of trout. Nature, London 173: 354.

Stuart, T.A. 1957. The migrations and homing behaviour of brown trout (Salmo trutta L.). Scientific Investigations. Freshwater and Salmon Fisheries Research. Scottish Home Department, Edinburgh. No. 18. 27pp.

Suzuki, R. & Fukuda, Y. 1971. Survival potential of F1 hybrids among salmonid fishes. Bulletin of the Freshwater Fisheries Research Laboratory (Tokyo) 21: 69-83.

Suzuki, R. & Fukuda, Y. 1973. Appearance and numerical characters of F1 hybrids among salmonid fishes. Bulletin of the Freshwater Fisheries Laboratory (Tokyo) 23: 5-32.

Symons, P.E.K. 1968. Increase in aggression and in strength of the social hierarchy among juvenile Atlantic salmon deprived of food. Journal of the Fisheries Research Board of Canada 25: 2387-2401.

Symons, P.E.K. & Heland, M. 1978. Stream habitats and behavioural interactions of underyearling Atlantic salmon (Salmon salar). Journal of the Fisheries Research Board of Canada 35: 175-183.

Taft, A.C. & Shapovalov, L. 1938. Homing instinct and straying among steelhead trout (Salmo gairdneri) and silver salmon (Oncorhynchus kisutch). California Fish and Game 24: 118-125.

Thomas, A.E., Banks, J.L. & Greenland, D.C. 1969. Effects of yolk sac absorption on the swimming ability of fall chinook salmon. Transactions of the American Fisheries Society 98: 406-410.

Tilzey, R.D.J. 1972. The Lake Eucumbene trout fishery. The Fisherman 4: 1-8.

Tinbergen, N. 1953. Fighting and threat in animals. New Biology 14: 9-24.

Unwin, M.J. 1984. Stream residence time, size characteristics and migration patterns of juvenile chinook salmon (Oncorhynchus tshawytscha) from a tributary of the Rakaia River. Fisheries Research Division, Ministry of Agriculture and Fisheries, New Zealand. M.S. copy.

Vandermeer, J.H. 1972. Niche theory. Annual Review of Ecology and Systematics 3: 107-132.

Vernon, E.H. 1957. Morphometric comparison of three races of kokanee (Oncorhynchus nerka) within a large British Columbia lake. 4Journal of the Fisheries Research Board of Canada 14: 573-598.

Volterra, V. 1926. Variations and fluctuations of the number of individuals of animal species living together. pp. 409-448. In: Chapman, R.N. (Ed.) Animal Ecology. McGraw-Hill Book Co., New York.

Wales, J.H. & Coots, M. 1955. Efficiency of chinook salmon spawning in Fall Creek, California. Transactions of the American Fisheries Society 84: 137-149.

Wangersky, P.J. 1978. Lotka-Volterra population models. Annual Review of Ecology and Systematics 9: 189-218.

Warner, K. 1963. Natural spawning success of landlocked salmon, Salmo salar. Transactions of the American Fisheries Society 92: 161-164.

Weatherly, A.H. & Lake, J.S. 1967. Introduced fish species in Australian inland waters. In Weatherly, A.H. (Ed.) Australian Inland Waters and their Fauna: Eleven Studies. A.N.U. Press, Canberra.

Weatherly, A.H. & Rogers, S.C. 1978. Some aspects of age and growth. pp. 52-74. In: Gerking, S.D. (Ed.), Ecology of Freshwater Fish Production. Blackwell Scientific Publications, Oxford.

Werner, E.E. & Hall, D.J. 1974. Niche shifts in sunfishes: experimental evidence and signifcance. Science 191: 404-406.

White, H.C. 1942. Atlantic salmon redds and artificial spawning beds. Journal of the Fisheries Research Board of Canada 6: 37-44.

White, T.C.R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia 33: 71-89.

Wickett, W.P. 1962. Environmental variability and reproduction potentials of pink salmon in British Columbia. pp. 73-86. In: Wilimovsky, N.J. (Ed.), A Symposium on Pink Salmon. H.R. MacMillan Lectures in Fisheries, University of British Columbia.

Wiens, J.A. 1977. On competition and variable environments. American Scientist 65: 590-597.

Wilson, D.S. 1975. The adequacy of body size as a niche difference. The American Naturalist 109: 769-784.

Zippin, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22: 82-90.

Appendix 1.1 BACK CALCULATION OF INCUBATION PERIODS

Spawning periods of adult female rainbow trout whose progeny emerged during selected portions of the emergence period were determined by back calculating incubation times from emergence to fertilization.

Lengths of incubation periods from fertilization to hatching were calculated using equation (1b) in Crisp (1981) in which:

$$\log D = b \log(T-\alpha) + \log a$$

where D is days from fertilization to 50% hatch, T is mean water temperature, α is a temperature correction factor, and b and $\log a$ are species specific constants given in Crisp (1981) Table 2. Lengths of incubation periods from fertilization to emergence were estimated approximately by multiplying the length of the period from fertilization to hatching (in days) by 1.714. This factor is the ratio of the former period over the latter, at 11°C, from the only complete data set from fertilization to emergence that I had available (obtained from records of the Department of Internal Affairs Ngongotaha hatchery, Rotorua, New Zealand). I added 15 days to these estimates since I considered the method may have underestimated the true incubation period by about that amount. I was of this opinion because when the method was applied to brown trout (using the appropriate ratio for that species, 1.706 at 11°C) it underestimated by about 15 days the observed incubation period to 50% emergence for brown trout, obtained in experimental Section 1 (Chapter IV, Section 4.6.1.2). In this particular comparison, the method actually underestimated the observed incubation period by 20 days, but five days were subtracted to allow for a delay in peak fry emergence which I considered had been caused by the inhibiting effects on emergence of high nocturnal illumination (caused by a full moon) which occurred

between 12 and 17 August 1981 (Fig. 4.7). Crisp (1980) developed the equation:

$$\log D_3 = -12.3324 \log(T + 75) + 25.6225$$

for estimation of the incubation period from fertilization to emergence (D_3) of brown trout. This method underestimated the observed incubation period of brown trout in the present study by 24 days (corrected to 19 days). Crisp and Ottaway (1981) found that this method underestimated observed dates of swim-up (emergence) usually by 21 days or more. The discrepancy between predicted and observed incubation times might, in part, be due to the physical difficulties of emergence from natural stream gravels delaying swim-up of wild fry.

Mean water temperatures used for the above calculations were obtained by averaging mean daily temperatures for each month, working backwards from the closest complete month to date of emergence, to the probable month of fertilization.

In back calculating approximate time of spawning of female rainbow trout whose progeny emerged on 26 November (the day of peak fry emergence) I subtracted five days from the estimated incubation period to allow for a minimum of five days delay in peak fry emergence caused by high nocturnal illumination occurring between 21 and 27 November (see Figure 5.1).

Appendix 2.1 Particle size composition (by dry weight (gm)) of samples of the three categories of spawning substrate.

Site	Grade A	Grade B			Grade C	
		1	2	3	1	2
	dry weight	dry weight	dry weight	dry weight	dry weight	dry weight
sieve size (mm)						
64	178.8	510.7	0	0	0	0
32	922.5	353.8	379.1	960.3	50.5	101.1
16	729.9	792.7	1113.2	445.3	555.9	816.4
8	419.0	622.4	861.8	814.0	1125.2	1292.8
4	143.6	383.0	598.5	622.4	885.8	718.2
2	69.9	197.9	340.9	405.9	464.8	361.7
1	35.0	70.9	216.4	188.9	173.8	150.8
0.5	23.1	25.1	117.5	94.6	101.5	112.1
0.25	29.0	15.0	77.8	69.0	80.9	136.7
0.125	17.2	11.7	60.9	39.9	26.0	58.2
0.063	3.2	2.4	33.8	6.8	6.4	6.8
>0.063	0.8	0.6	20.8	3.3	1.8	2.8
d_{84}	56	70	11.7	47	17.3	11
d_{16}	10.1	5.7	2.52	2.82	2.76	2.72

Appendix 2.2 Records of redds constructed on eight regularly observed sites during the 1980 spawning season.

Site	Redd	Construction date (1980)	Estimated date of emergence (1980)	Area (m^2)	Proportion of redd superimposed (%) during the period of incubation for which observations were made						Proportion (%) of incubation period observed
					1x	2x	3x	4x	5x	Total	
1a	1	~10 May	15 Aug	1.488	40	7	0.3			47.3	69
	2	23 May	16 Aug	0.881	21	5				26	64
	3	7 Jun	4 Sep	0.388	100					100	45
	4	17 Jul	3 Oct	0.940							0
2	1	~12 May	14 Aug	1.091	57	31	12			100	100
	2	7 Jun	4 Sep	0.517	59	8	15	18		100	100
	3	21 Jul	5 Oct	2.220	20	18	14	1		53	89
	4	28 Jul	9 Oct	0.469	30	30	5			65	81
	5	14 Aug	21 Oct	0.700	39	29				68	65
	6	14 Aug	21 Oct	0.231	68					68	65
	7	25 Aug	29 Oct	0.293	46					46	51
	8	25 Aug	29 Oct	0.296	79					79	51
	9	27 Sep	15 Nov	0.552							0
	10	27 Sep	15 Nov	0.431							0
3a	1	~10 May	15 Aug	1.540	24	19	33	4	0.3	80.3	100
	2	7 Jun	4 Sep	1.445	36	50	11	0.4		97.4	83
	3	17 Jun	10 Sep	1.022	57	7	0.7			64.7	75
	4	17 Jun	10 Sep	0.319	41	59				100	75
	5	7 Jul	26 Sep	1.904	15					15	54
	6	7 Jul	26 Sep	0.392	76					76	54
	7	17 Jul	3 Oct	0.997	100					100	44
	8	17 Jul	3 Oct	0.365	100					100	44

Cont'd over....

Site	Redd	Construction date (1980)	Estimated date of emergence (1980)	Area (m^2)	Proportion of redd superimposed (%) during the period of incubation for which observations were made						Proportion (%) of incubation period observed
					1x	2x	3x	4x	5x	Total	
4	1	~ 8 May	13 Aug	1.669	72					72	100
	2	8 Jun	5 Sep	1.366						0	100
	3	7 Jul	26 Sep	1.655	49	23				72	100
	4	17 Jul	3 Oct	1.166	34					66	100
	5	14 Aug	21 Oct	1.101	2	2				4	88
	6	4 Sep	5 Nov	1.180	2					2	63
	7	4 Sep	5 Nov	0.788	10	6				16	63
	8	19 Sep	13 Nov	1.152	34	39				73	44
	9	29 Sep	17 Nov	1.480	56					56	29
	10	13 Oct		0.836							
5	1	~10 May	~15 Aug	1.170						0	100
	2	10 May	15 Aug	0.409						0	100
	3	25 Aug	29 Oct	1.449	13	78				91	38
	4	4 Sep	5 Nov	1.113	85	7				92	24
	5	4 Sep	5 Nov	1.719	44					44	24
	6	19 Sep	13 Nov	1.136	6					6	0 approx.
	7	19 Sep	13 Nov	1.112						0	0
6	1	~10 May	~15 Aug	1.313	41	58				99	100
	2	19 Jun	12 Sep	1.339	87					87	100
	3	1 Jul	20 Sep	1.759						0	100
	4	14 Aug	22 Oct	0.354						0	88
	5	19 Sep	13 Nov	1.543	100					100	44
	6	13 Oct		2.216						0	0

Cont'd over/....

Site	Redd	Construction date (1980)	Estimated date of emergence (1980)	Area (m^2)	Proportion of redd superimposed (%) during the period of incubation for which observations were made						Proportion (%) of incubation period observed
					1x	2x	3x	4x	5x	Total	
1b	1	14 Aug	22 Oct	0.946	33	5				38	88
	2	25 Aug	29 Oct	0.608	10					10	75
	3	25 Aug	29 Oct	1.214	23	16	42			81	75
	4	30 Aug	2 Nov	1.978	20	48				68	69
	5	4 Sep	5 Nov	1.150	83					83	63
	6	10 Sep	9 Nov	1.990	11					11	55
	7	Checked on 13 Oct									
3b	1	25 Aug	29 Oct	1.640	71	25				96	75
	2	25 Aug	29 Oct	0.801	35	11				46	75
	3	29 Sep	17 Nov	0.730	9					9	29
	4	29 Sep	17 Nov	0.776	56					56	29
	5	13 Oct		2.154							0

Appendix 2.3 Survival of eggs from deposition to fry emergence for various species of Salmonidae (expanded from Irvine 1978).

Species	% survival	Reference
chum salmon	5.7 - 31.1	Hunter 1959
pink salmon	0.2 - 32.3	Merrel 1962, Wicket 1962, McNeil 1962
sockeye salmon	1.8 - 19.3	Foerster 1968, Pritchard 1947, Moring and Lantz 1975
chinook salmon	7.0 - 32.0	Wales and Cootes 1955
" "	35.5 - 61.1	Unwin 1984
Atlantic salmon	92.0	Warner 1963
brown trout	61 - 89	Hobbs 1948
brook trout	90.0	McFadden 1961
Yellowstone cutthroat trout	25.0 - 40.0	Ball and Cope 1961
steelhead	75.0 - 86.3	Briggs 1953, Shapovalov and Taft 1954

Appendix 2.4 Monthly mean lengths (95% confidence limits) of brown (arithmetic mean) and rainbow trout (geometric mean) in each electrofishing sampling section over three summers.

Month and sampling date	Section	1979-1980				1980-1981				1981-1982			
		Rainbow		Brown		Rainbow		Brown		Rainbow		Brown	
		$\bar{L}$	n	$\bar{L}$	n	$\bar{L}$	n	$\bar{L}$	n	$\bar{L}$	n	$\bar{L}$	n
November	1	33.0 ± 2.2	30							32.5 ± 0.8	254	49.0	2
3 - 1979	2	32.7 ± 1.7	59	43.8 ± 4.5	5	31.9 ± 0.8	441	58.0 ± 1.9	22	36.2 ± 0.9	454	55.2 ± 3.6	10
13 - 1980	3a/3b	35.1 ± 2.7	29			31.1 ± 0.9	342	54.0	1	39.0 ± 1.7	100	54.9 ± 1.6	26
15 - 1981	4												
December	1	33.3 ± 0.9	362			34.3 ± 0.6	452			30.8 ± 0.4	762	65.0	1
10 - 1979	2	35.9 ± 0.8	572	63.5 ± 4.0	4	32.7 ± 0.4	750	65.9 ± 3.5	21	33.9 ± 0.6	724	71.5 ± 4.2	12
11 - 1980	3a/3b	38.3 ± 1.4	220	53.7 ± 8.0	3	34.5 ± 0.8	416	69.5	2	31.7 ± 0.4	1052	76.3 ± 4.4	10
16 - 1981	4	34.0 ± 1.7	73	51.0									
January	1	48.4 ± 0.8	388			48.6 ± 0.8	573	81.0 ± 5.9	3	42.2 ± 0.8	588	86.8 ± 5.5	6
16 - 1980	2	44.8 ± 1.0	520	85.0 ± 14.2	4	51.5 ± 1.2	510	81.8 ± 4.3	18	46.5 ± 0.9	512	87.9 ± 5.4	9
15 - 1981	3a/3b	48.7 ± 1.4	217	70.0	2	48.8 ± 2.1	196	75.0 ± 7.6	4	41.7 ± 0.8	380	88.3 ± 5.6	8
18 - 1982	4	43.9 ± 1.9	71	67.8 ± 4.8	4								
February	1	55.0 ± 1.6	179			60.8 ± 1.2	404	92.5	2				
14 - 1980	2	57.7 ± 1.3	388	110.8 ± 9.7	6	61.9 ± 1.2	540	95.1 ± 6.8	12				
12 - 1981	3a/3b	56.6 ± 1.2	266	70.5	2	56.6 ± 2.3	161	88.3 ± 4.9	8				
	4	51.3 ± 1.2	142	75.7 ± 5.0	13								
March	1	65.2 ± 1.2	293	91.0	1	71.3 ± 1.5	268	105.5 ± 8.3	4	63.8 ± 2.1	183	111.6 ± 6.9	5
12 - 1980	2	63.8 ± 1.6	319	121.5 ± 29.9	4	71.8 ± 1.3	406	104.6 ± 4.4	8	66.1 ± 1.3	452	118.7 ± 8.0	9
16 - 1981	3a/3b	65.0 ± 1.4	243	95.0 ± 11.2	7	65.1 ± 3.2	131	99.9 ± 7.1	7	67.3 ± 2.3	167	114.1 ± 4.9	11
17 - 1982	4	63.4 ± 1.6	77	86.0 ± 4.9	3								
April	1	68.3 ± 1.3	229	138.0	1	77.8 ± 1.9	203	121.0	2	63.2 ± 1.8	128	121.3 ± 14.3	4
14 - 1980	2	70.5 ± 1.7	311	135.2 ± 10.4	6	78.4 ± 1.8	325	118.8 ± 9.4	5	62.4 ± 1.4	216	133.0	1
15 - 1981	3a/3b	73.1 ± 2.1	169	101.0 ± 11.1	6	73.7 ± 3.2	185	107.9 ± 6.2	12	63.0 ± 1.4	147	114.5	2
16 - 1982	4	72.1 ± 2.4	48	90.3 ± 6.4	3								
June	1					72.2 ± 3.1	41	114.5					
16 - 1981	2					78.9 ± 5.2	48	135.2 ± 7.5	5				

Section 3a was sampled during 1979-1980 whereas Section 3b was sampled during 1980-1981 and 1981-1982.

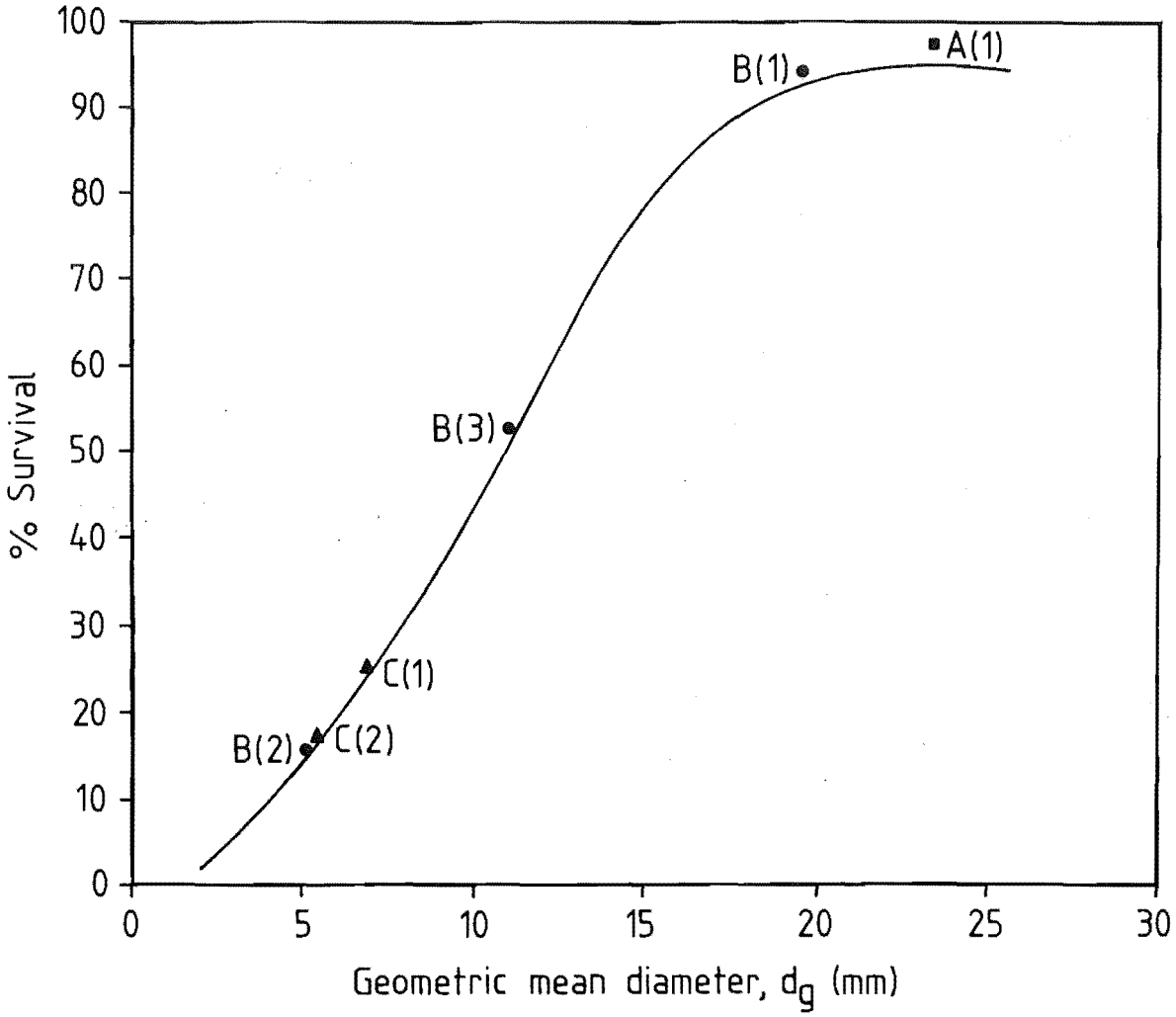
Appendix 2.5 Number and mean size of fish used in the behavioural experiments conducted in the observation troughs during the spring of 1981.

	ALLOPATRY						SYMPATRY					
	Experiment No. & description	Species	Replicate No.	No.	Mean length (range) (mm)	Mean weight (range) (gm)	Experiment No. & description	Species	Replicate No.	No.	Mean length (range) (mm)	Mean weight (range) (gm)
SERIES I	1) Brown and rainbow fry in allopatry	Rainbow	1	40	28.6 (26.6-30.6)	0.16 (0.12-0.22)	2) Brown and rainbow fry in sympatry	Rainbow	1	20	29.6 (27.0-32.4)	0.19 (0.13-0.28)
			2	40	31.3 (29.0-33.9)	0.22 (0.16-0.30)			2	20		
		Brown	1	40	28.2 (26.2-30.1)	0.17 (0.13-0.21)		Brown	1	20	30.0 (27.4-32.8)	0.22 (0.15-0.30)
			2	40	31.6 (29.0-33.7)	0.25 (0.19-0.31)			2	20		
							3) Brown and rainbow fry in sympatry (rainbow fry with prior residence)	Rainbow	1	20	Fish from experiment 1.	
									2	14		
								Brown	1	20	29.6 (27.8-31.4)	0.20 (0.16-0.25)
									2	14	32.7 (29.3-34.8)	0.30 (0.22-0.36)
							4) Brown and rainbow fry in sympatry (brown fry with prior residence)	Rainbow	1	20	29.3 (27.6-31.5)	0.18 (0.15-0.24)
									2	14	32.6 (29.4-34.8)	0.26 (0.17-0.36)
								Brown	1	20	Fish from experiment 1.	
									2	14		
SERIES II	2) Brown and rainbow fingerlings in allopatry	Rainbow	1	16	55.3 (48.9-61.1)	1.56 (1.02-2.14)	3) Brown and rainbow fingerlings in sympatry	Rainbow	1	8	54.5 (50.5-57.7)	1.59 (1.27-1.92)
			2	16	54.0 (50.0-58.4)	1.57 (1.17-2.03)			2	8	53.1 (50.8-55.2)	1.44 (1.22-1.62)
		Brown	1	16	48.9 (45.2-54.6)	1.11 (0.87-1.56)		Brown	1	8	54.6 (51.8-57.9)	1.67 (1.35-1.93)
			2	16	55.9 (47.4-61.6)	1.68 (1.01-2.32)			2	8	52.8 (49.5-56.4	1.50 (1.18-1.86)

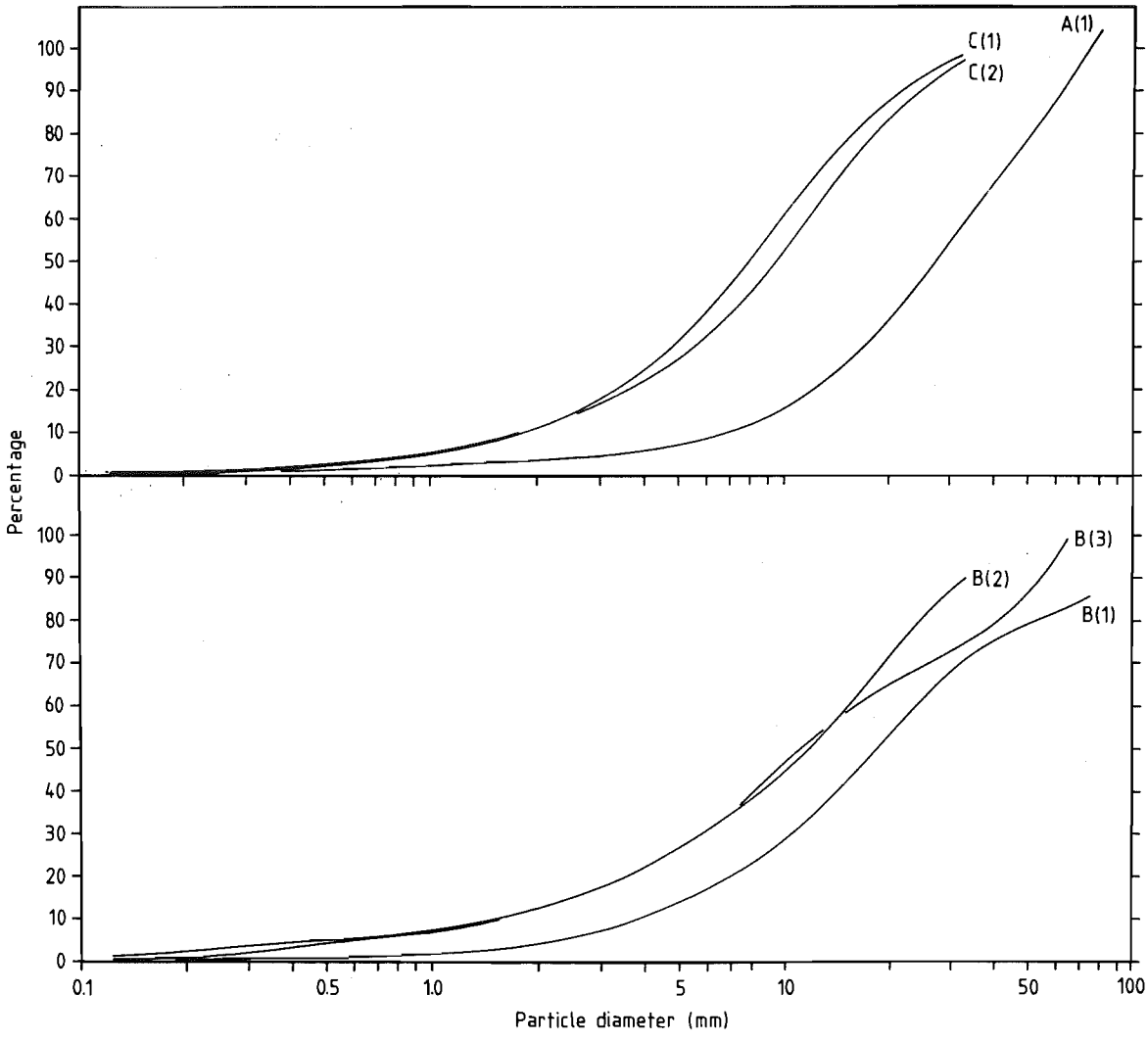
Cont'd over/....

SERIES II

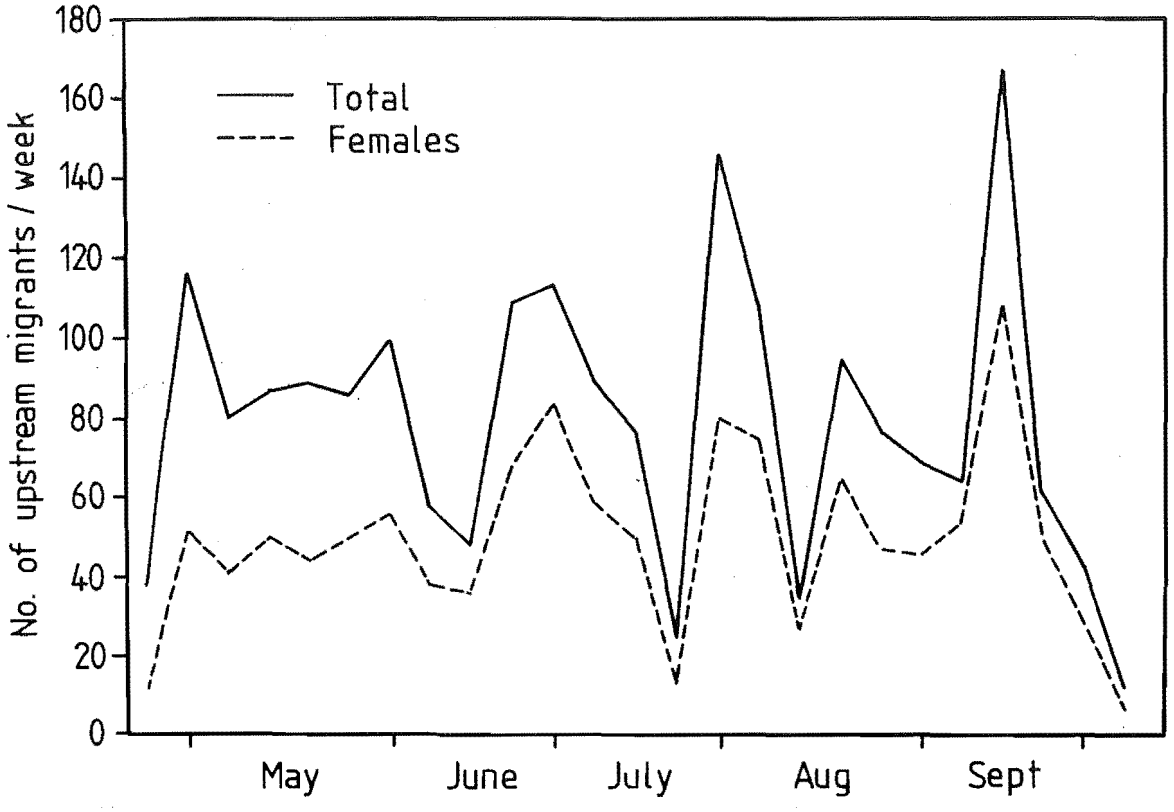
ALLOPATRY						SYMPATRY					
Experiment No. & description	Species	Replicate No.	No.	Mean length (range) (mm)	Mean weight (range) (gm)	Experiment No. & description	Species	Replicate No.	No.	Mean length (range) (mm)	Mean weight (range) (gm)
1) Rainbow fry in allopatry	Rainbow	1	40	28.9 (27.0-30.7)	0.17 (0.13-0.22)	4) Rainbow fingerlings mixed with rainbow fry	Rainbow fingerlings	1	10	45.3 (43.1-50.3)	0.85 (0.71-1.23)
		1	40	29.9 (27.6-32.0)	0.18 (0.12-0.24)			2	10	52.9 (48.5-57.3)	1.53 (1.12-2.10)
							Rainbow fry	1	30	29.1 (27.4-30.5)	0.17 (0.13-0.23)
								2	30	30.1 (28.5-31.7)	6.10 (0.15-0.27)
						5) Brown fingerlings and rainbow fry in sympatry	Brown fingerlings	1	10	53.5 (48.8-55.8)	1.50 (1.12-1.84)
								2	10	53.0 (50.1-55.3)	1.62 (1.40-1.79)
							Rainbow fry	1	30	29.9 (28.2-31.8)	0.20 (0.16-0.25)
								2	30	29.6 (27.3-32.5)	5.90 (0.13-0.25)
						6) Rainbow and brown fingerlings and rainbow fry in sympatry	Rainbow fingerlings	1	5	60.3 (56.7-62.5)	2.05 (1.70-2.36)
								2	5	61.2 (57.3-66.8)	2.16 (1.78-2.65)
							Brown fingerlings	1	5	60.1 (59.0-64.5)	2.09 (1.64-2.60)
								2	5	60.3 (58.4-66.6)	2.12 (1.47-2.81)
							Rainbow fry	1	30	30.7 (28.5-33.8)	0.21 (0.16-0.35)
								2	30	30.7 (28.5-33.6)	0.21 (0.16-0.28)



Appendix 3.1 Predicted percent embryo survival for substrate categories from Scotts Creek according to the relationship between percent embryo survival and substrate composition expressed in geometric mean diameter.
From Shirazi and Seim (1979).



Appendix 3.2 Cumulative distribution of particle diameter of samples of three categories of spawning gravel from Scotts Creek.



Appendix 3.3 Weekly number of upstream migrant rainbow trout entering Scotts Creek in 1962. From Moore et al. (1962).